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Detecting Change in Benthic Communities at San Cristobal Reef in La Parguera, Puerto Rico, 2007-2009

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DETECTING CHANGE IN BENTHIC COMMUNITIES AT SAN CRISTOBAL REEF IN LA PARGUERA, PUERTO RICO, 2007-2009

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by

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ABSTRACT

Detecting change in benthic communities at San Cristobal reef, La Parguera, 2007-2009

by

Jeremy M. Kerr

Master of Science in Coastal and Watershed Science and Policy

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The ecological integrity of coral reef ecosystems around the world and their associated goods and services are threatened by the synergistic effects of natural and anthropogenic disturbances. Benthic community composition at San Cristobal reef in La Parguera, Puerto Rico, was monitored from 2007 to 2009 using SCUBA-based photoquadrat surveys, and assessed for change over time using a model-comparison approach, which accounted for spatial autocorrelation. Additionally, the optimal point densities and optimal photoquadrat totals necessary to detect change reliably in proportional cover were investigated. Benthic community structure was similar at all sampling sites throughout the study; algal and sand classes were the dominant classes with non-scleractinian invertebrate classes having similar or greater proportional cover than scleractinian classes. Detected changes in scleractinian classes, including *Acropora* and *Montastraea* classes, were lower than detected changes in other invertebrate classes. To investigate optimal sampling intensity, one-hundred re-samples of the point overlays were drawn for ten point densities, ranging from five points quadrat^{-1} to 90 points quadrat^{-1}, and seven photoquadrat totals, ranging from two photoquadrats to 50 photoquadrats. The change for estimated proportional benthic cover between 2007 and 2008 for four benthic cover classes (*M. annularis*, *P. astreoides*, poriferans, and sand) within each re-sample were assessed for change. The minimum number of points required to detect change reliably depended on the cover class and desired detection sensitivity. Low point densities (e.g., five points photoquadrat^{-1} or 20 points m^{-2}) were sufficient to detect large changes in classes with high proportional benthic cover while high point densities (e.g., 70 points photoquadrat^{-1} or 280 points m^{-2}) were needed to detect small changes in benthic cover classes with low proportional cover reliably. Intermediate point densities (e.g., 50 points photoquadrat^{-1} or 200 points m^{-2}) enabled detection of either small changes in classes with high proportional cover or large changes in classes with low proportional cover. Lower quadrat totals (e.g., 20 photoquadrats 100 m^{-2}) were sufficient to detect large changes, and higher quadrat totals (e.g., 40 photoquadrats 100 m^{-2}) were necessary to detect small changes reliably. Therefore, researchers should be conservative when determining sampling intensity and select higher point densities (e.g., 50-70 points photoqradrat^{-1}) and higher photoquadrat totals because a less intense sampling regime (e.g., five points photoquadrat^{-1} or 20 photoquadrats) could result in inaccurate proportional cover estimates and unreliable detection of change. Programs monitoring benthic community structure in coral reefs using points overlaid on photoquadrats should determine the appropriate point density and number of photoquadrats per unit area based on proportional cover of the benthic classes, minimum change in cover to be detected, and the spatial autocorrelation distance,

and should account for spatial autocorrelation between points when performing statistical analyses.

TABLE OF CONTENTS

PAGE

LIST OF TABLES

PAGE

LIST OF FIGURES

PAGE

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INTRODUCTION

The consensus among coral reef researchers is that the health of coral reef ecosystems around the world has declined over the last half century and the declines will continue into the near future (Wilkinson 2000, 2008; Gardner et al. 2003; Hughes et al. 2003; Wilkinson and Souter 2008). The declines in ecosystem health have been attributed to the synergistic effects of storm damage (Gardner et al. 2005), nutrient enrichment (Hughes 1994; Szmant 2002), large-scale bleaching events (Wilkinson and Souter 2008), disease outbreaks (Muller et al. 2008), loss of herbivores (Lessios et al.1984; Gardner et al. 2003), and predator outbreaks (Faure 1989) altering benthic community structure by reducing live scleractinian cover and increasing macroalgae cover. These shifts in community structure threaten the goods and services human communities derive from coral reefs (Moberg and Folke 1999; Pandolfi et al. 2003) leading to a need to expand conservation efforts (Hughes et al. 2003).

A necessary aspect to implementing and evaluating conservation actions is establishing a measurement of baseline community structure and monitoring change in that community structure over time through *in situ* sampling (Hill and Wilkinson 2004). Sampling methods for benthic communities of coral reefs include manta tows (e.g., Baker et al. 1990), swimming surveys (DeVantier et al. 2006), belt transects (Bries et al. 2004), linear transects (Steiner and Kerr 2005), point intercept transects (Hass et al. 2010), video transects (Japp and McField 2001), photo transects (Done et al. 2007), and photoquadrats (Preskitt et al. 2004). The samples provide data on benthic community structure over time and statistical analysis of the data is used to infer change in the sampled communities.

A variety of statistical methods are used to evaluate whether or not change has occurred and each of these involves some assumptions or constraints that are often not easily met (Zuur et al. 2007, 2009). In particular, sampling units collected by divers in marine systems are often close together because of the difficulty of covering large areas underwater. This close proximity means that the necessary assumption of independent residual variation between sample units does hold without special consideration. This assumption implies that the residual variation in one observation is not dependent on the residual variation of any other observation.

Ecological data often violate the assumption of independence between observations due to the presence of spatial autocorrelation (Legendre and Fortin 1989; Legendre 1993; Legendre et al. 2002; Zuur et al. 2007, 2009; Kissling and Carl 2008). Legendre (1993) defined spatial autocorrelation as, "the property of random variables taking values, at pairs of locations a certain distance apart, that are more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected for randomly associated pairs of observations." In other words, residual variation in a datum (Y_1) at one location either positively or negatively affects residual variation in a datum (Y_2) at another location, thus contradicting the assumption of independence between observations. Under the assumption of independence, each observation contributes one full degree of freedom for the statistical test; however, a lack of independence means that each observation contributes a fraction of a degree of freedom (Legendre and Fortin 1989; Legendre 1993). Failure to account for spatial autocorrelation leads to inflated Type I error rates due to underestimated confidence intervals (Legendre et al. 2002), biased correlation and regression parameters (Kissling and Carl 2008), and can reverse the direction of estimated effects of explanatory variables on response variables (Kühn 2007). Consequently, the presence of spatial autocorrelation is problematic for inference and hypothesis testing using a frequentist approach to statistical analysis (Dormann et al. 2007; Kissling and Carl 2008).

One approach to account for spatial autocorrelation in ecological data is to incorporate spatial autocorrelation into the statistical models (Legendre and Fortin 1989; Dormann et al. 2007; Kühn 2007; Zuur et al. 2007, 2009). Regression models can take the form of autoregressive models (Legendre and Fortin 1989; Dormann et al. 2007; Kissling and Carl 2008) in which a variable describing the spatial autocorrelation between observations is incorporated into the regression model as an explanatory variable (Legendre and Fortin 1989; Dormann et al. 2007). A specific case of an autoregressive model is the autologistic regressive model, which is a logistic regression model that incorporates the spatial autocovariance variable (Augustin et al.1996).

Spatial correlation between sampling units is seldom accounted for during analyses of change in benthic communities indicating that these analyses can be

improved. By accounting for spatial correlation, inferences of change in benthic communities will be more reliable thereby improving the reliability of information available to resource managers on a system's current status and changes within that system. This study aimed to improve analysis of change in proportional benthic cover by a) developing a method for evaluating change given spatially correlated data acquired from points overlaid on photoquadrats; b) developing a method for optimizing sampling designs using points overlaid on photoquadrats, and c) applying the methods to a case study at San Cristobal reef in La Parguera, Puerto Rico. This location was selected because it is included in an ongoing effort (since 2004) by researchers from the National Aeronautics and Space Administration (NASA) and the University of Puerto Rico at Mayaguez (UPRM) to remotely-sense coral reef communities in the La Parguera area. They collected hyperspectral imagery of the reefs using NASA's Airborne Visible/Infrared Imaging Spectrometer (AVIRIS) (Guild et al. 2006, 2008; Lobitz et al. 2009), flown at low altitude on-board NASA's Twin Otter aircraft, and coincident field data. Their work contributes to a multi-agency effort to assess change in benthic communities following the Caribbean bleaching event in 2005. Due to historic benthic community composition (Ballantine et al. 2005), the 2005 bleaching event, and storm surge generated by Hurricane Dean in August 2007, I postulated that benthic community structure in La Parguera reefs would change over time following these events. Specifically, proportional cover of macroalgae would be high at the beginning of the study and decrease over time while the proportional cover of scleractinians would begin low and, in the absence of major disturbances, increase each year. The observed changes in proportional cover were expected to be small, thus sampling intensity needed to be high to detect change reliably. The high sampling intensity led to spatial correlation between sampling units, which was then accounted for during statistical analysis.

METHODS

Overall approach

The overall approach developed for this study involved sampling of benthic communities, assessing the magnitude of change between samples, and quantifying the evidence supporting whether change did or did not occur, and, post hoc, considering the optimal sampling design. The benthic communities were sampled using points overlaid on photoquadrats; these point overlays were aggregated to provide estimated proportional cover for each benthic cover class within each sample site for each year. Autologistic regression models that account for spatial autocorrelation between points were then fit to the point data. Next, the change and the strength of evidence supporting change were assessed by using information theoretic (model comparison) techniques on the models. The theoretically optimal sampling design was then determined by re-sampling the complete data set to reflect differing point densities (points photoquadrat^{-1}) and quadrat totals. Finally, the information theoretic technique was applied to each re-sampled data set thereby enabling identification of point densities and quadrat totals that produced reliable results.

Study location

La Parguera is located along the southwestern coast of Puerto Rico (Figure 1). The area contains patch reefs that protect the shoreline from strong wave action resulting in large seagrass beds on the leeward sides of the reefs and a shoreline dominated by mangroves (Guild et al. 2006; Ryan et al. 2008). Benthic communities in this area have been previously affected by bleaching and storm events. Historically, bleaching events coinciding with elevated and prolonged water temperatures were observed in 1969, 1987, 1990, 1995, and 1998 (Winter et al. 1997; Garcia-Sais et al. 2005) and cases of minor to moderate bleaching were also observed in 1981, 1987, 1989, 1991, 1992, and 1993 (Winter et al. 1997). This area has also been impacted by hurricanes with Garcia-Sais et al. (2005) suggesting that hurricanes may, "be the main factor in the decimation of elkhorn coral (*Acropora palmata*) biotopes in [Puerto Rican] reefs." In 1963, Hurricane Edith, a category 1 hurricane, passed within 49 nmi of La Parguera resulting in little damage to terrestrial systems and extensive alteration of the benthos within several patch

reefs (Glynn et al. 1964). Although a relatively weak storm, the hurricane toppled and fragmented large colonies of *A. palmata* in the fore reef zones of several reefs, and distributed *Porites porites* fragments throughout the back reef zones (Glynn et al. 1964).

More recently, the La Parguera area experienced a bleaching event in 2005 and wave action generated by the passing of Hurricane Dean to the south in 2007. In 2005, anomalously high sea surface temperatures (i.e., >30° C) were observed in the western Atlantic Ocean and northeastern Caribbean Sea, and they persisted for 4 to 6 months in some locations (Donner et al. 2007; Wilkinson and Souter 2008). The prolonged exposure to elevated ocean temperatures resulted in severe bleaching of scleractinians throughout the eastern tropical Atlantic (Miller et al. 2006; Donner et al. 2007; Whelan et al. 2007; Oxenford et al. 2008; Muller et al. 2008; Rowlands et al. 2008; Steiner and Kerr 2008; Wilkinson and Souter 2008). In August 2007, Hurricane Dean, the strongest hurricane of the 2007 season, formed in the Atlantic Ocean and traversed the Caribbean Sea eventually making landfall in Mexico as a Category 5 Hurricane (Franklin 2008). The storm passed, "about 180 nmi south of Puerto Rico" (Franklin 2008). The wave action produced by the storm toppled and fragmented colonies of *A. cervicornis* and *A. palmata* at San Cristobal reef (R. Armstrong, pers. comm.).

San Cristobal is a medium-sized patch reef in comparison to surrounding patch reefs (Figures 1 and 2). Before 2005, overall live scleractinian cover in La Parguera reefs was 18% with *Montastraea* spp. being the most abundant live scleractinian cover (Ballantine et al. 2008). Live *Acropora* spp. cover was abundant in the shallows areas, and the platform of San Cristobal contained a large stand and numerous small stands of *A. cervicornis* (Ballantine et al. 2008). During the 2005 bleaching event, researchers observed bleaching in colonies of 52 scleractinian species in the La Parguera area and outbreaks of several diseases (Ballantine et al. 2008). Following the bleaching event and the disease outbreaks, mass mortality of live scleractinian cover occurred, and sexual reproduction in *Acropora* spp. and *Montastraea* spp. was almost non-existent (Ballantine et al. 2008). Additionally, the large *A. cervicornis* stand in San Cristobal's platform suffered near 100% mortality following the disturbances in 2005 (Ballantine et al. 2008).

Figure 1: Mosaic of AVIRIS flight lines over the La Parguera area in southwestern Puerto Rico. The data were collected in December 2005 through a combined effort of NASA and UPRM researchers. The AVIRIS instrument was flown aboard NASA's Twin Otter aircraft providing a nominal spatial resolution of 4-m by 4-m for each pixel. San Cristobal reef and the location of UPRM research station on Isla Magueyas are labeled.

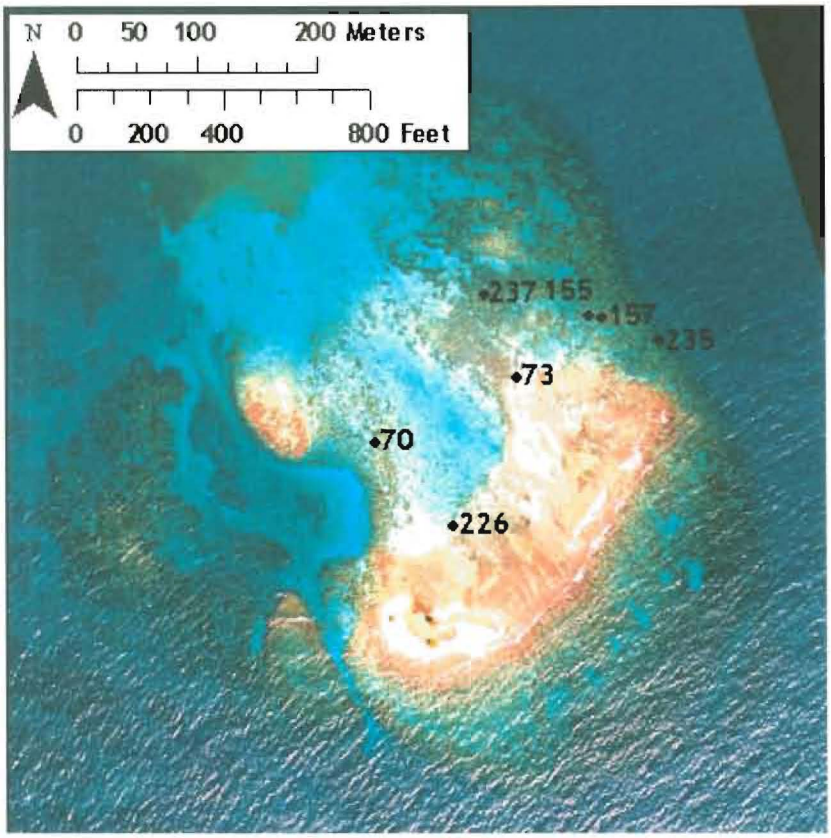

Figure 2: Aerial photograph of San Cristobal reef with a nominal spatial resolution of 67 cm by 67 cm. The sampling sites for this study are identified.

Sampling sites

The seven sampling sites in this study were selected to provide ground-truth data on the benthic composition of shallow communities at San Cristobal reef for comparison with the results of spectral unmixing of hyperspectral data (Guild et al. 2006, 2009). As such, the sampling design used to estimate proportional cover and detect change in benthic communities was established prior to the start of the present study. Six of the seven sampling site were sampled while free diving, and the seventh site (Site 235) was sampled while scuba diving. The sampling sites were located in the back reef and reef slope zones with no sampling locations located on the seaward side (i.e., southern side) of the reef crest. Site 70, located on the western side of the back reef zone near the transition to the reef slope zone, was primarily composed of massive coral colonies (*Montastraea* spp., primarily) and gorgonian colonies interspersed by sand. Site 73 was composed of

coral rubble from both branching and massive scleractinians, macroalgae, and sand; it was located in the eastern side of the back reef zone. Sites 155 and 157 were adjacent sites located within the eastern reef slope, near the transition to back reef zone, primarily composed of *A. palmata* rubble, poriferans, and *Porolithon*. Site 226, located in the south of the back reef zone, was primarily composed of branching scleractinian rubble and sand. Site 235 was the deepest sampling site and was located in the eastern reef slope zone near the forereef; it was composed of massive coral colonies (*Montastraea* spp., primarily) interspersed with sand. Site 237, the northern most sampling site, was located in the back reef zone, and it was composed of branching scleractinian and gorgonian rubble, gorgonians, encrusting poriferans, the seagrass *Thalassia testudinum*, and sand.

Transects

Within each sampling location, divers placed a central 10 m transect line (i.e., primary base line). Figure 3 shows the idealized version of the sampling design. At the ends of the base line, GPS coordinates were taken using a Garmin GPS76CSx handheld unit (Garmin 2009) in a small dry bag and a differential GPS (dGPS) attached to a small boat, and permanent markers were placed in or on the reef. The GPS points and markers were used to relocate the endpoints of the base line in subsequent years. After data collection along the base line was completed, a 10-m transect line was placed perpendicularly so that its center (i.e., 5-m mark) intersected the base line at its 3-m mark (Figure 3). After data collection along this second transect line was completed, the transect line was moved to the 7-m mark, and data was collected along this transect line. To avoid overlap in the photoquadrats, divers did not collect photoquadrats between the 4 m and 6 m marks on the perpendicular transect lines, thus providing a 50 cm buffer on these perpendicular lines around their intersection with the base line.

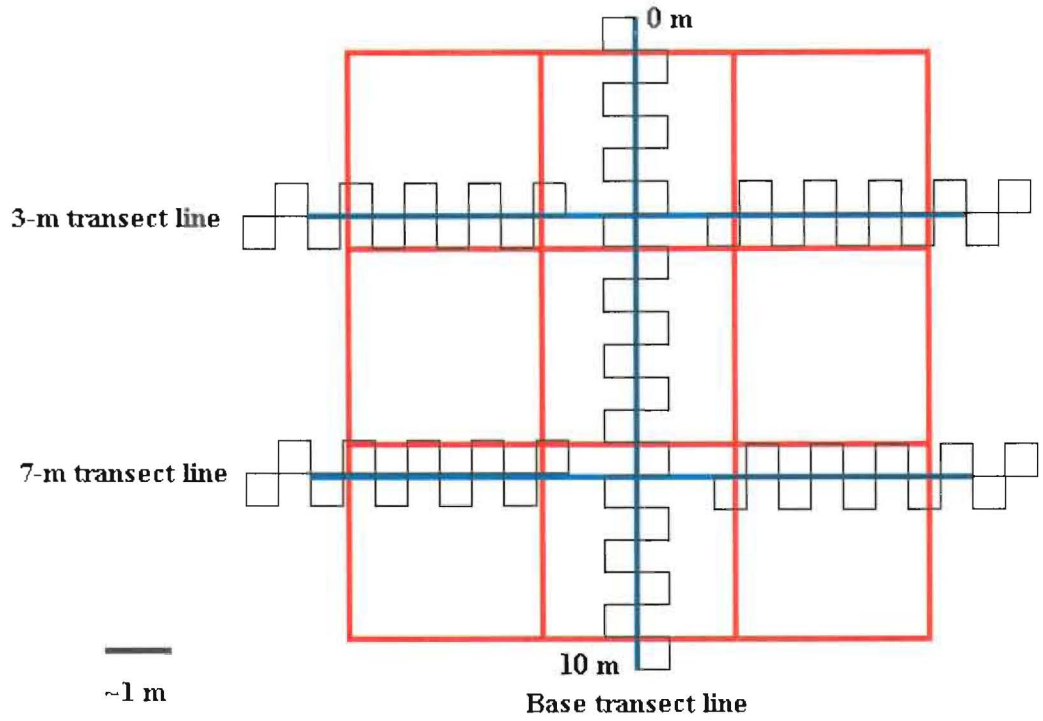

Figure 3: A diagram of *in situ* sampling method for a 3-pixel by 3-pixel area (~81 m^2). Each red box represents a theoretical 3-m by 3-m pixel (~9 m^2) within an AVIRIS image. Blue lines represent 10-m transects. Small black boxes represent the placement of a 0.5-m by 0.5-m (0.25 m^2) quadrat for a photoquadrat. One hundred points were placed within each photoquadrat.

Photoquadrats

Photoquadrats (i.e., underwater images of quadrats) were used to provide data on benthic community structure (Figure 4). They were collected along the base transect and along each perpendicular transect using a digital camera in an underwater housing. Photoquadrats were 0.5-m by 0.5-m squares covering an area of 0.25-m^2 and made out of PVC pipe. The first quadrat was placed on the right side of the base line with the bottom left corner placed at the 0-m mark (Figure 3). A photoquadrat was taken with a digital camera encased in an underwater housing. After the photoquadrat was completed, a diver moved the quadrat to the left side of the base line with the bottom right corner of the quadrat placed at approximately the 0.5-m mark and another photoquadrat was taken. This process was repeated along the length of the base line resulting in 20 photoquadrats. After the collection of photoquadrats along the base line was completed, the first

perpendicular transect line was centered at the 3-m mark on the base transect line. Photoquadrats were taken along the length of this transect line resulting in 20 photoquadrats. After collection of photoquadrats along this perpendicular line was completed, the process was repeated along the second perpendicular transect line, centered at the 7-m mark on the base transect line. This overall process resulted in approximately 60 photoquadrats for each sampling location during each sampling year.

Figure 4: Photoquadrat collected from Site 235 at San Cristobal reef, December 2007. Each leg of the quadrat is 50 cm providing a framed area of 0.25 m^2 (2500 cm^2).

Photoquadrat Rectification

The quadrats in the resulting photoquadrats were oblique and did not appear square due to camera angle and diver positioning (Figure 4). The photoquadrats were rectified using the ERDAS Imagine software suite (ERDAS 2009) so that quadrats appeared as squares (Figure 5). For each photoquadrat, eight ground control points

(GCPs) were used to correct the photoquadrats: one at each corner and one approximately in the middle of each leg. A second-order nearest neighbor image resampling with the GCPs was performed to rectify the photoquadrats. Photoquadrats were not rectified if the corners of the quadrat, used as references for the rectification process, were not visible within the image. When overlap between separate photoquadrats was observed, the photoquadrats chosen for rectification provided the greatest number of photoquadrats (and thus the greatest total sampling area) with no overlap between rectified photoquadrats.

Figure 5: Photoquadrat (Figure 4) collected from Site 235 at San Cristobal reef, December 2007, after rectification. The quadrat appears closer to a square than in the unrectified version.

Benthic cover estimates

Points were overlaid on the photoquadrats using the Coral Point Count with Excel extensions (CPCe) software package (Kohler and Gill 2006). For each rectified

photoquadrat, a stratified random point distribution using 100 points was created (Figure 6). The points were stratified as such: the photoquadrat was divided into a grid of 10 boxes by 10 boxes with each box being ~25 cm^2, and 1 point was randomly placed within each box. This is an option when placing points within CPCe. The extent of the point distribution was delineated by manually creating a border that coincided with the area framed by the quadrat.

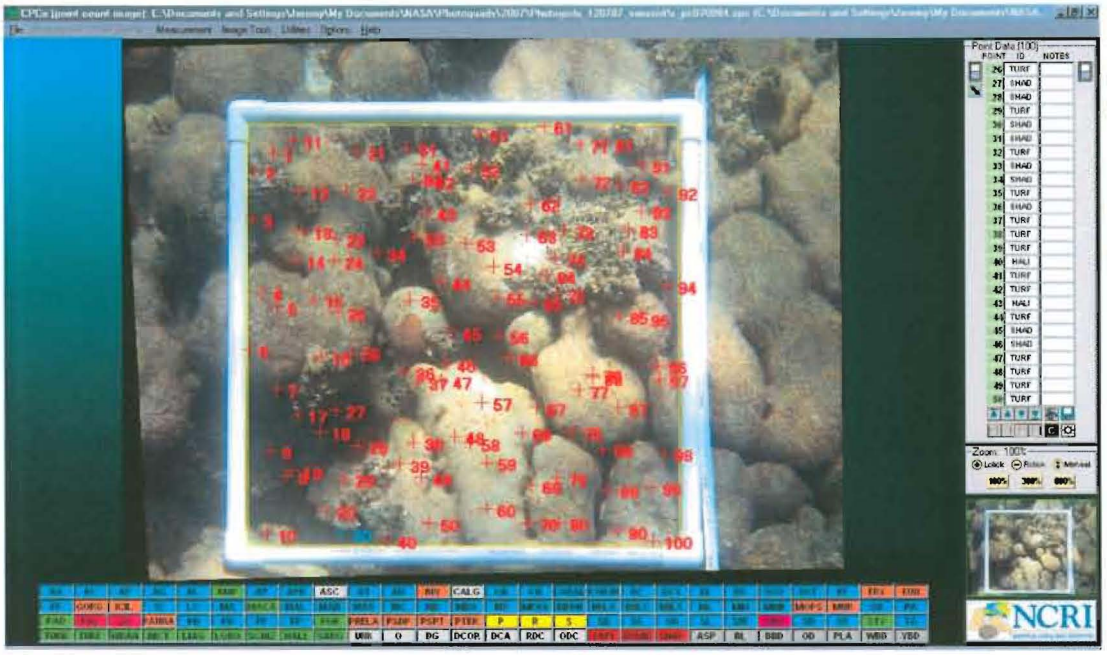

Figure 6: Rectified photoquadrat from Site 235 at San Cristobal reef, December 2007, (Figure 5) with 100 stratified random points overlaid in CPCe (Kohler and Gill 2006).

The benthic cover class under each point was assigned using the CPCe default classes (Figure 7). Benthic class identifications were based on Humann and DeLoach (2002). Macroalgae were identified to Genus, and scleractinians were identified to species. These levels of identification were not possible at all times due to image distortion, shading effects, or inability to distinguish identifiable characteristics. The generic macroalgae and coral categories were used for points that overlaid scleractinian colonies or macroalgae thalli that could not be identified to the species or Genus level. The Shadow class was assigned anytime shadowing effects prevented benthic cover class

identification at that point. The Wand class was assigned when a point was placed over the quadrat or a diver's hand. Proportional benthic cover was estimated using the R statistical program (R Development Core Team 2009).

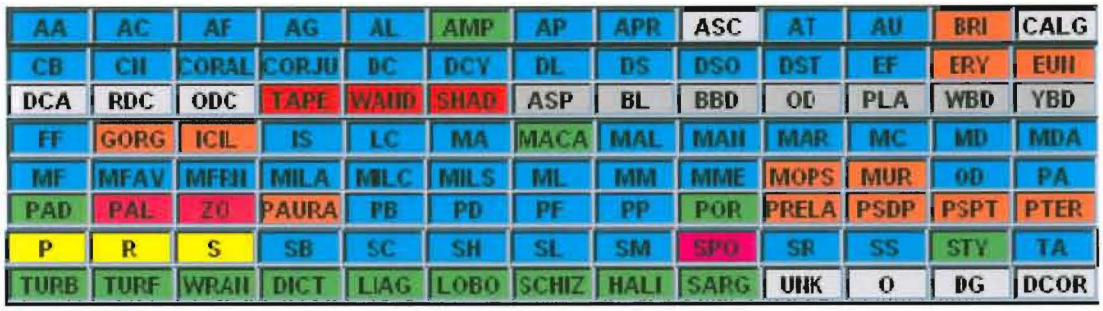

Figure 7: Default benthic class codes for CPCe (Kohler and Gill 2006).

Spatial Autocorrelation

The coral reef benthos is a mosaic of abiotic and biotic patches whose location on the reef is shaped through various physical and biological forces that occur over variable spatial scales, and as such, statistical analyses of samples from the reef benthos need to acknowledge the spatial nature of the observations. Spatial autocorrelation occurs when an observation at one location either positively or negatively affects the observation at another point (Legendre 1993), and it is often observed in ecological data (Zuur et al. 2007, 2009). The presence of spatial autocorrelation within the raw data and model residuals was demonstrated by plotting covariance against separation distance (between two observations) creating correlograms (Legendre and Fortin 1989). To account for this, the spatial autocorrelation for each point was estimated, thereby creating a value that could be included as an explanatory variable in the models. This was achieved by creating a correlogram for each benthic cover class in each year of the data and fitting a function to the spatial autocorrelation values within the correlogram to model the decay of spatial autocorrelation with increasing distance. An exponential function and an inverse-distance function were compared to identify which of the two better described the decay of spatial autocorrelation. Estimated covariance between two points was calculated from the fitted spatial autocorrelation model as a function of separation distance,

calculated as the Euclidean distance between the two points. For a given point, the spatial autocorrelation with neighboring points was calculated as the average autocorrelation with points within a 100 cm radius. Creation and plotting of correlograms and modeling of spatial autocorrelation were performed using the R statistical program (R Development Core Team 2009).

Statistical Model

To assess the occurrence of change in proportional benthic cover between two years, two statistical models were compared using a model-comparison approach (described in detail below). This approach estimates which of the competing models best fits the data. For each benthic cover class, two logistic models were compared where each model represented a different, competing hypothesis for the presence of a benthic cover class at a point. The two models were

$$\text{M0: } \Pr(Y_i = 1) = \text{logit}^{-1}(\beta_0 + \beta_s \cdot sac)$$
$$\text{M1: } \Pr(Y_i = 1) = \text{logit}^{-1}(\beta_0 + \beta_s \cdot sac + \beta_y \cdot year)$$

where

$$\text{logit}^{-1}(-x) = \frac{1}{1+\exp(-x)},$$

M0 and M1 are Models 0 and 1, respectively, Y_i is a binary response at point i, sac is the spatial autocovariance variable, $year$ is a binary response for time, and β is an estimable parameter, and x is a linear combination of covariates being input into the logit function. This input varies with the model. Model 0 represented a situation where no change due to time occurred, and Model 1 represented a situation where change due to time did occur.

The sampling unit for analysis was the point (i.e., a single point from the points overlaid on the photoquadrats). For each point, a binary response (i.e., presence or absence resulting in $Y_i = 0$ or $Y_i = 1$, respectively) was created for the benthic cover class being tested for change. Given this type of response, the logistic model needed to be used to analyze the influence of year on the presence of a benthic cover class at a given point. A spatial autocovariance variable was incorporated into the logistic regression, thereby making the resulting model an autologistic model (Augustin et al. 1996). Time was

represented through a binary variable for year (i.e., $year = 0$ or $year = 1$); the first year in a tested data set had year equal to 0 and the second year had year equal to 1.

Model Selection

An information-theoretic (model comparison) approach based on Akaike Information Criteria (AIC ; Akaike 1973; Burnham and Anderson 2002) was used to assess the occurrence of change. The AIC weight (w_i), which represents the probability that each model was the best-fit model, was calculated for each model, and an evidence ratio (ER) was calculated to quantify the strength of the evidence supporting the best-fit model (Burnham and Anderson 2002). For descriptive purposes, evidence ratios were interpreted within four categories to provide a qualitative description of the level of evidence supporting the selected candidate model (Table 1) following the methods of Croyle (2009). This model comparison process was performed using the R statistical program (R Development Core Team 2009).

Table 1: Qualitative descriptions used to describe evidence ratio values (as described in Croyle 2009), that indicate the amount of evidence supporting a selected model, which represent whether change did or did not occur.

Evidence	Evidence Ratio	Description
Minimal	$1 < ER \leq \sqrt{10}$	The selected model barely has more supporting evidence than the other candidate model indicating high uncertainty in the detection of change.
Substantial	$\sqrt{10} < ER \leq 10$	The selected model has substantially more supporting evidence than the other candidate model indicating substantial support for the selected model.
Strong	$10 < ER \leq 100$	The selected model has strong supporting evidence compared to other candidate model indicating strong support for the selected model.
Decisive	$ER > 100$	The selected model is decisively better than the other candidate model indicating decisive evidence for a selected model.

$\sqrt{10} \approx 3.16$

Determining optimal sampling density

A sensitivity analysis was performed to examine how point density (i.e., points photoquadrat^{-1}) and photoquadrat totals affected the estimated benthic cover and model selection results. Point densities in this analysis ranged from 5 points photoquadrat^{-1} to 90 points photoquadrat^{-1}, and photoquadrat totals ranged from 2 photoquadrats to 50 photoquadrats (Table 2). One hundred random samples were drawn from a larger data set (100 points photoquadrat^{-1} data set from Site 235 between 2007 and 2008 with 57 and 59 total photoquadrats, respectively) for each point density and photoquadrat total to create 100 new data sets on which the model selection process to detect change was performed. Four benthic cover classes common to reef locales in the Caribbean (*M. annularis*, *P. astreoides*, poriferans, and sand) were included in this sensitivity analysis. These classes were selected because they represented a variety of 1) change in proportional cover estimates between sampling, 2) actual detection of change, and 3) evidence supporting the detection of change.

Table 2: The point densities and number of photoquadrats used in the sensitivity analysis.

Value	Resample sizes
Number of points per photoquadrat	5, 10, 20, 30, 40, 50, 60, 70, 80, 90
Number of photoquadrats	2, 5, 10, 20, 30, 40, 50

RESULTS

Photoquadrats

A total of 1192 photoquadrats collected from San Cristobal reef were used to calculate benthic cover estimates and to evaluate change (Table 3). In 2007, 2008, and 2009, 405, 414, and 373 photoquadrats were rectified, respectively. The number of photoquadrats within a year at a site ranged from 45 to 63 (Figure 8). Not all collected photoquadrats were rectified, due to image quality issues associated with collection in the field (see 'Photoquadrat Rectification' above for greater detail), and used for analysis resulting in this variation.

Table 3: The number of photoquadrats and the number of points per sampling location for the years 2007, 2008, and 2009.

	No. Photoquadrats				No. Points			
Location	**2007**	**2008**	**2009**	**Total**	**2007**	**2008**	**2009**	**Total**
70	56	61	52	**169**	5600	6100	5200	**16,900**
73	60	63	59	**182**	6000	6300	6900	**18,200**
155	61	58	49	**168**	6100	5800	4800	**16,800**
157	57	59	48	**164**	5700	5900	4800	**16,400**
226	59	54	60	**173**	5900	5400	6000	**17,300**
235	57	59	45	**161**	5700	5900	4500	**16,100**
237	55	60	60	**175**	5500	6000	6000	**17,500**
Total	**405**	**414**	**373**	**1192**	**40,500**	**41,400**	**37,300**	**119,200**

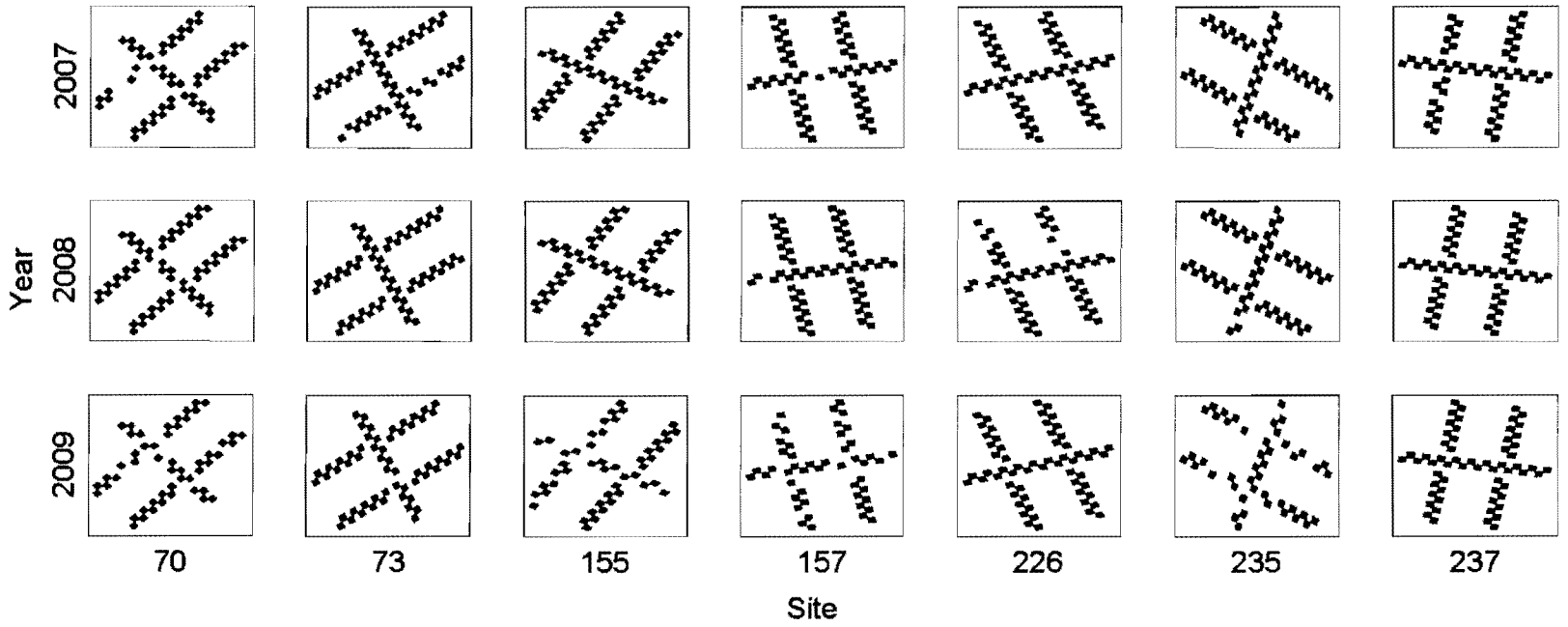

Figure 8: Relative placement of rectified photoquadrats used to detect change in benthic cover classes within each of the seven sampling sites at San Cristobal reef for 2007 through 2009. Missing photoquadrats were the result of image quality issues associated with field collection, such as blurring, overlap between photoquadrats, and quadrats being out of frame.

Genera and species presence

Seventeen scleractinian species were identified under the points (Table 4; Figure 9a-d). Although *Montastraea annularis* and *M. faveolata* could be distinguished in some images, they could not be clearly distinguished in all images, thus they were grouped into the *M. annularis*-complex category (hereafter-referred to as *M. annularis*) for analysis. *Porites porites*, *P. divaricata*, and *P. furcata* were not separated during identification, thus they are all grouped as *P. porites*. Image blurring and shading within images caused some scleractinians under a point to be unidentifiable; these points were assigned the generic "scleractinian" category.

Macroalgae identified in the photoquadrats included turf algae and the genera *Dictyota*, *Halimeda*, and *Porolithon* (Figure 9e, f). Epiphytic growth, image distortion due to camera movement (i.e., diver movement), and subject movement (i.e., macroalgae swaying in the current) resulted in points that could be identified as macroalgae but could not be identified to genus level, thus they were identified as the "macroalgae" class. The genera *Dictyota* and *Halimeda* were included in this macroalgae class during analysis. In 2009, numerous *Cyanobacteria* thalli with a "fuzzy brown" appearance occurred at Site 73, and they were subsequently grouped into the "macroalgae" category.

Non-scleractinian, non-algal classes were identified for points within the photoquadrats, and they were grouped into generic classes for the analyses. The hydrocoral, *Millepora*, was identified in the study, but the lack of development in the colonies prevented identification to the species level. Zoanthids identified within photoquadrats included *Palythoa caribaeorum* and *Zoanthus pulchellus*. Gorgonians included *Erythropodium caribaeorum* and the genera *Gorgonia*, *Pseudoplexaura*, and *Pseudopterogorgia*. Sponge genera included, but were not limited to, *Agelas*, *Anthosigmella*, and *Cliona*.

Table 4: Scleractinian species identified under points overlaid on photoquadrats from San Cristobal reef. Status as of April 2010 under the Endangered Species Act (ESA) as described by the National Marine Fisheries Service (Acroporids: NOAA 2006; Other scleractinians: NOAA 2010). Predominant colony morphology observed at San Cristobal reef, and habitat and abundance in the Caribbean as described by Veron (2000a, 2000b, 2000c) and Humann and DeLoach (2002).

Scleractinian species	ESA status	Morphology	Habitat	Abundance
Acropora cervicornis	Threatened	Branching	Shallow outer reef slopes, lagoons	Common
Acropora palmata	Threatened	Branching	Upper to mid-reef slopes; lagoons	Common
Acropora prolifera	Not listed	Branching	Shallow reef slopes; lagoons	Uncommon
Agaricia agaricites	Not listed	Submassive	Shallow reef environments	Common
Colpophyllia natans	Not listed	Massive	Shallow reef environments	Common
Dendrogyra cylindrus	Candidate	Pillar	Most reef environments	Uncommon
Dichocoenia stokesii	Candidate	Massive	Most reef environments	Uncommon
Diploria clivosa	Not listed	Massive	Most reef environments	Common
Diploria labyrinthiformis	Not listed	Massive	Shallow reef environments	Common
Diploria strigosa	Not listed	Massive	Most reef environments	Common
Meandrina meandrites	Not listed	Submassive	Most reef environments	Uncommon
Montastraea annularis	Candidate	Massive	Most reef environments	Common
Montastraea cavernosa	Not listed	Massive	All reef environments	Common
Porites astreoides	Not listed	Massive	All reef environments	Common
Porites porites	Not listed	Branching	Shallow protected reef environments	Common
Siderastrea siderea	Not listed	Massive	Shallow reef environments	Common

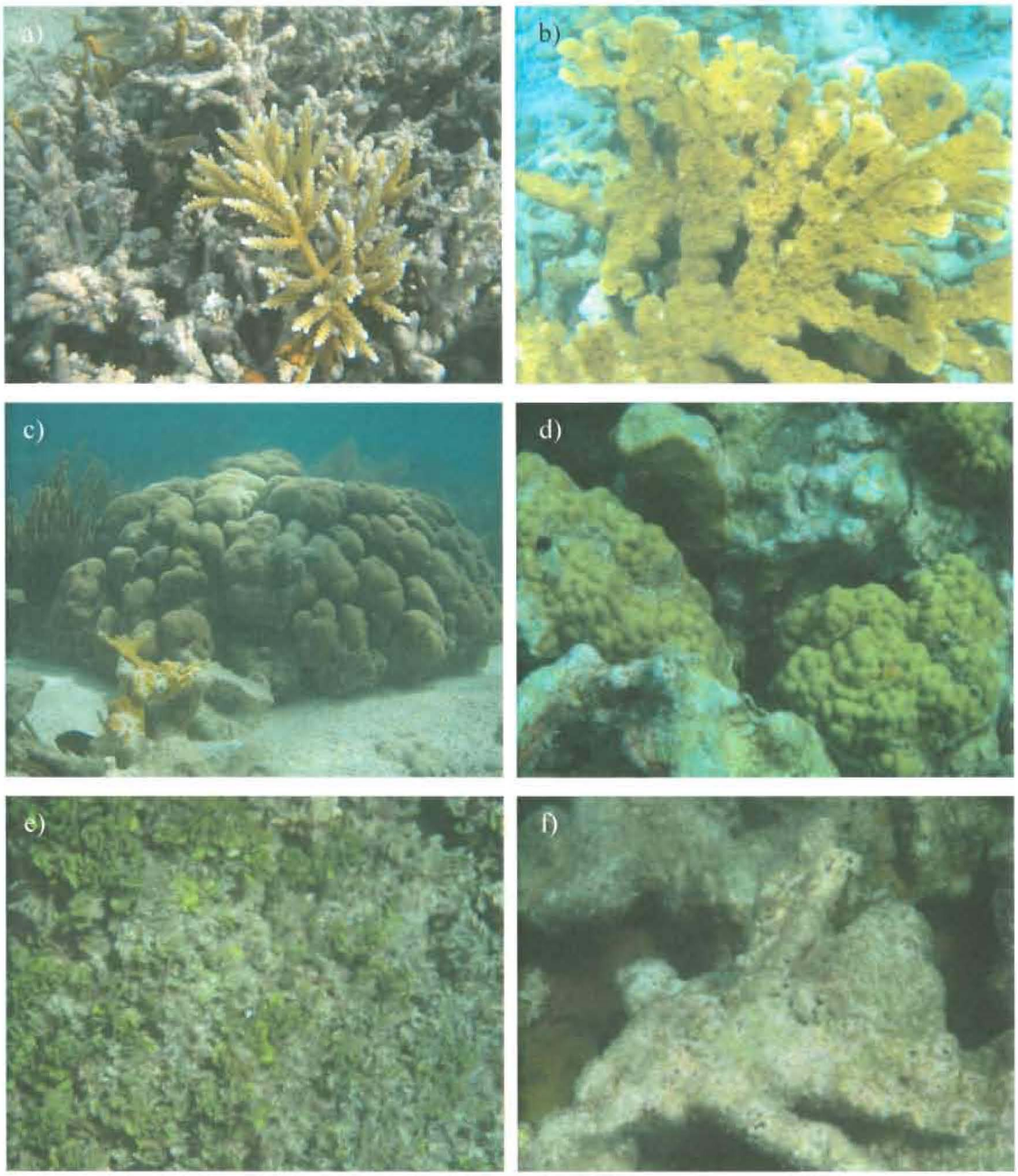

Figure 9: Examples of observed benthic cover classes. a) An *Acropora cervicornis* colony surrounded by dead *A. cervicornis* covered by turf algae. b) An *Acropora palmata* colony. c) A *Montastraea annularis* colony surrounded by sand with an *Acropora* recruit in the foreground and gorgonian colonies in the background. d) *Porites astreoides* colonies and a *Montastraea* colony surrounded by coral skeleton covered by turf algae. e) *Halimeda* thalli. f) Coral skeleton covered by a mix of turf algae, *Porolithon*, and poriferans. (Photo credits: John Preston a; Liane Guild b, d, e, f; Jeremy Kerr c)

Spatial autocorrelation

Spatial autocorrelation was present in the raw data (Figure 10) for all benthic cover classes and model residuals for logistic models containing no spatial autocorrelation term (Figure 11). The spatial autocorrelation range differed among classes. For example, it was approximately 10 cm for *P. astreoides* and 80 cm for sand in the raw data at site 235 in 2007 and 2008 (Figure 10). Due to the presence of spatial autocorrelation in the raw data and models' residual values, an inverse distance model and an exponential model for the spatial autocovariance structure were visually compared for the 100 points photoquadrat^{-1} data set (Figure 11) to determine which model better reduced spatial autocorrelation within the autologistic models' residual values. This assured that the residuals were spatially independent and thus valid sample units for the statistical analysis. It was found that unaccounted spatial autocorrelation was clearly reduced in the models' residual values by adding a spatial autocorrelation term into the model (Figure 11), and both spatial autocorrelation models (inverse distance and exponential decay) had similar reductions in the unaccounted spatial autocorrelation (Figure 11). The exponential model was used to model the spatial autocovariance structure within the autologistic models in the subsequent model selection processes for change detection and in the sensitivity analysis.

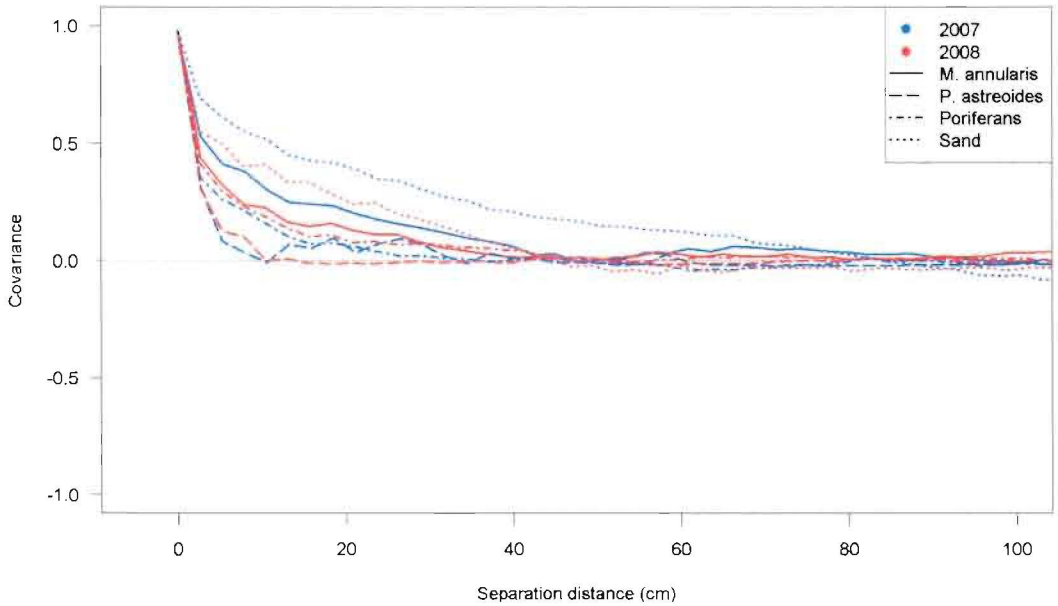

Figure 10: Example correlograms for raw data for the *M. annularis*, *P. astreoides*, poriferan, and sand classes at Site 235 between 2007 (blue) and 2008 (red).

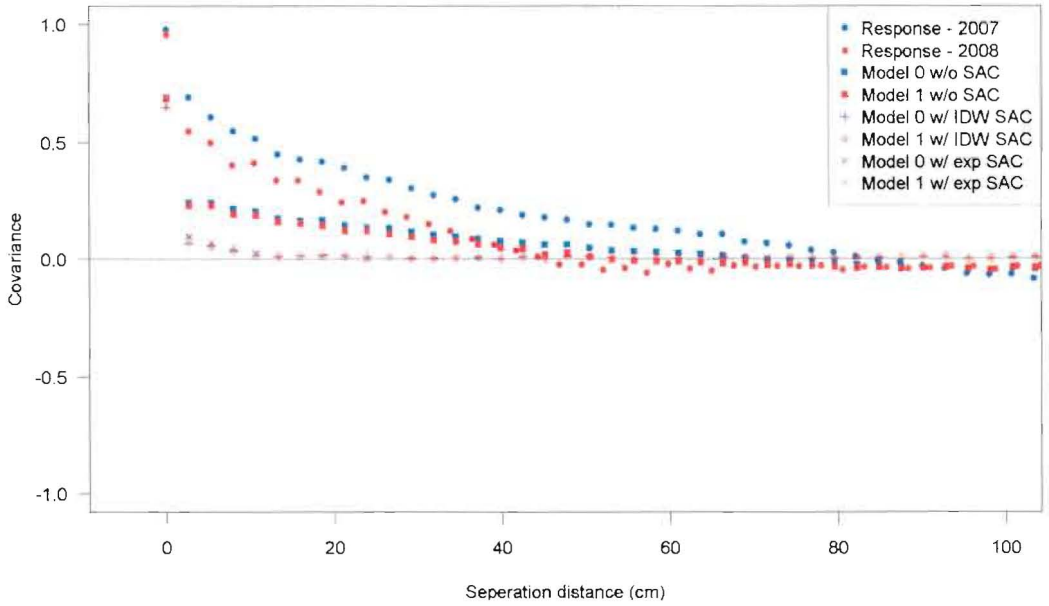

Figure 11: Example correlograms for the sand class at Site 235 between 2007 and 2008 illustrating that incorporating a spatial autocorrelation term reduced autocorrelation in the model residuals; this assured that the residuals are spatially independent and thus valid sample units for the statistical analysis. Included are raw data (•), model residuals containing no spatial autocorrelation variable (■), model residuals containing an inverse distance spatial autocorrelation variable (+), and model residuals containing an exponential decay spatial autocorrelation variable (×) for 100 points photoquadrat^{-1}.

Changes in benthic cover classes

Overall patterns in detected change in general benthic cover classes differed among classes, among years, and among sampling sites (Figure 12a). Sampling sites were most often dominated by macroalgae cover with scleractinians having the lowest proportional cover class. Proportional cover of sand and non-scleractinian invertebrates was often greater than the scleractinian cover.

A common pattern of change among the scleractinian classes did not occur. Proportional cover for scleractinians was less than 10% at six sites with Site 235, the deepest site, having proportional scleractinian cover less than 15% in all three years (Tables 5 and 6). The detected changes in scleractinian classes were relatively smaller than those detected in the other classes (Tables 5 and 6). *M. annularis* was the dominant scleractinian at five sites (Figure 12b). *A. cervicornis* was the dominant scleractinian at

Site 237, and *P. porites* was the dominant scleractinian at site 226 (Figure 12b). *M. annularis* was evaluated for change at five sites (Tables 5 and 6), and detected changes for this species were decreases at Site 70 in the first period between 2007 and 2008 (M1, $\Delta p = -1.21\%$, $ER = 26.92$) and at Site 73 during the following period 2008 and 2009 (M1, $\Delta p = -0.24\%$, $ER = 35.04$). *A. cervicornis* was evaluated for change at four sites (Tables 5 and 6). In the first period, the only detected change for this species was a decrease at site 226 (M1, $\Delta p = -0.07\%$, $ER > 100$). Increases were detected at Sites 73 (M1, $\Delta p = 0.19\%$, $ER > 100$), 157 (M1, $\Delta p = 0.29\%$, $ER = 3.83$), and 237 (M1, $\Delta p = 0.35\%$, $ER = 10.83$) in the second period. *P. astreoides* and *P. porites* occurred at five or more sites in all three years. For the five sites at which *P. astreoides* was evaluated for change, increases were detected in the first period at Site 73 (M1, $\Delta p = 0.06\%$, $ER = 12.17$) and Site 235 (M1, $\Delta p = 0.34\%$, $ER > 100$). *P. porites* was evaluated for change at four sites. A decrease was detected for this species at Site 70 from 2007 to 2008 (M1, $\Delta p = -0.04\%$, $ER = 8.00$), and from 2008 to 2009, increases were detected at Sites 155 (M1, $\Delta p = 0.05\%$, $ER = 27.93$)and 235 (M1, $\Delta p = 0.57\%$, $ER = 3.47$). *A. palmata* was observed at two sites in all three years; and it was evaluated for change at Site 155, where the only detected changed was an increase from 2008 to 2009 (M1, $\Delta p = 0.59\%$, $ER > 100$). Of the 12 other scleractinian species observed (Table 4), three were not evaluated for change because they had less than 0.1% estimated proportional cover for the years they were observed (*C. natans*, *D. stokesii*, and *M. meandrites*). Change was not detected in four other scleractinians (*A. prolifera*, *A. agaricites*, *D. clivosa*, and *M. cavernosa*) during either period. An increase in *D. cylindrus* cover was detected at Site 157, the only site where it was observed, from 2007 to 2008 (M1, $\Delta p = 0.20\%$, $ER = 35.08$). *D. labyrinthiformis* was observed at Sites 157 and 235. It was evaluated for change at Site 235 only, where an increase was detected in the second period (M1, $\Delta p = 0.15\%$, $ER = 29.67$). *D. strigosa* was observed in 3 locations (Sites 73, 226, and 237). The only detected change for this class was a decrease at Site 73 in the second period (M1, $\Delta p = -0.61\%$, $ER = 35.04$). *S. siderea* was observed at Sites 155, 157, and 235, and its estimated proportional cover was found to increase in

the first period (M1, $\Delta p = 0.16\%$, $ER = 3.51$) and decrease in the second period (M1, $\Delta p = -0.13\%$, $ER = 6.90$) at Site 155.

Proportional cover for non-scleractinian invertebrates was often greater than the proportional cover of scleractinian classes (Figure 12a). Among the non-scleractinian invertebrates, gorgonians and poriferans had the greatest proportional cover (Figure 12c). Poriferan proportional cover generally increased through the study, and zoanthid cover was similar throughout (Figure 12c). During the first period, increases were detected for poriferans at Sites 73 (M1, $\Delta p = 0.61\%$, $ER > 100$), 157 (M1, $\Delta p = 8.12\%$, $ER > 100$), 235 (M1, $\Delta p = 10.73\%$, $ER = 8.05$) and 237 (M1, $\Delta p = 2.33\%$, $ER > 100$), and a decrease was detected at Site 70 (M1, $\Delta p = -1.54\%$, $ER = 97.45$). For this class in the second period, increases were detected at Sites 70 (M1, $\Delta p = 1.03\%$, $ER > 100$), 73 (M1, $\Delta p = 6.00\%$, $ER > 100$), 155 (M1, $\Delta p = 6.93\%$, $ER > 100$), 226 (M1, $\Delta p = 2.27\%$, $ER > 100$), and 237 (M1, $\Delta p = 10.25\%$, $ER > 100$). For the zoanthid class, the only detected changes were increases at Site 235 from 2007 to 2008 (M1, $\Delta p = 0.13\%$, $ER = 8.23$) and at Site 226 the following period (M1, $\Delta p = 3.11\%$, $ER > 100$). Gorgonian cover was generally consistent throughout the study (Figure 12c). For this class, changes detected between 2007 and 2008 were mostly negative (Table 5); however, between 2008 and 2009, all detected changes were positive (Table 6). The decreases detected in the first period occurred at Sites 70 (M1, $\Delta p = -2.02\%$, $ER > 100$), 155 (M1, $\Delta p = -0.30\%$, $ER > 100$), 226 (M1, $\Delta p = -1.51\%$, $ER > 100$), and 237 (M1, $\Delta p = -7.98\%$, $ER = 65.16$). The lone increase was detected at Site 235 (M1, $\Delta p = 2.66\%$, $ER = 7.70$). The increases detected during the second period occurred at Sites 155 (M1, $\Delta p = 2.64\%$, $ER > 100$), 226 (M1, $\Delta p = 1.56\%$, $ER > 100$), and 237 (M1, $\Delta p = 13.28\%$, $ER = 4.99$).

Turf algae was the dominant class at all sampling sites throughout the study except for Site 73 in 2009 (Figure 12d). In general, proportional cover of turf algae increased in the first period and then decreased during the second period (Tables 5 and 6). For this class, increases were detected at Sites 70 (M1, $\Delta p = 20.37\%$, $ER > 100$) and 73 (M1, $\Delta p = 12.42\%$, $ER = 34.15$) from 2007 to 2008, and decreases were detected at Sites

73 (M1, $\Delta p = -25.47\%$, $ER > 100$) and 237 (M1, $\Delta p = -14.15\%$, $ER = 5.02$) from 2008 to 2009. Macroalgae cover, which included *Halimeda* and *Dictyota*, and *Porolithon* cover were consistent throughout the study. For the macroalgae class from 2007 to 2008, a decrease was detected at Site 73 (M1, $\Delta p = -1.95\%$, $ER > 100$), and increases were detected at Sites 157 (M1, $\Delta p = 6.51\%$, $ER = 56.06$) and 226 (M1, $\Delta p = 5.55\%$, $ER > 100$). During the following period, increases were detected at Sites 73 (M1, $\Delta p = 35.88\%$, $ER > 100$), 155 (M1, $\Delta p = 2.29\%$, $ER > 100$), 226 (M1, $\Delta p = 0.82\%$, $ER = 4.84$) and 237 (M1, $\Delta p = 3.27\%$, $ER > 100$), and a decrease was detected at Site 235 (M1, $\Delta p = -0.20\%$, $ER > 100$). A *Cyanobacteria* bloom was observed at Site 73 in 2009, and it was grouped into the macroalgae class. This grouping resulted in a sharp increase in macroalgae cover from 2008 to 2009 making it the dominant benthic cover class at this site for 2009 (Figure 12d). From 2007 to 2008, increases were detected in the *Porolithon* class at 235 (M1, $\Delta p = 1.98\%$, $ER > 100$) and 237 (M1, $\Delta p = 0.59\%$, $ER > 100$). During the following period, increases for this class were detected at Site 157 (M1, $\Delta p = 1.90\%$, $ER > 100$) and 237 (M1, $\Delta p = 0.75\%$, $ER > 100$), and a decrease was detected in Site 226 (M1, $\Delta p = -0.21\%$, $ER = 3.27$).

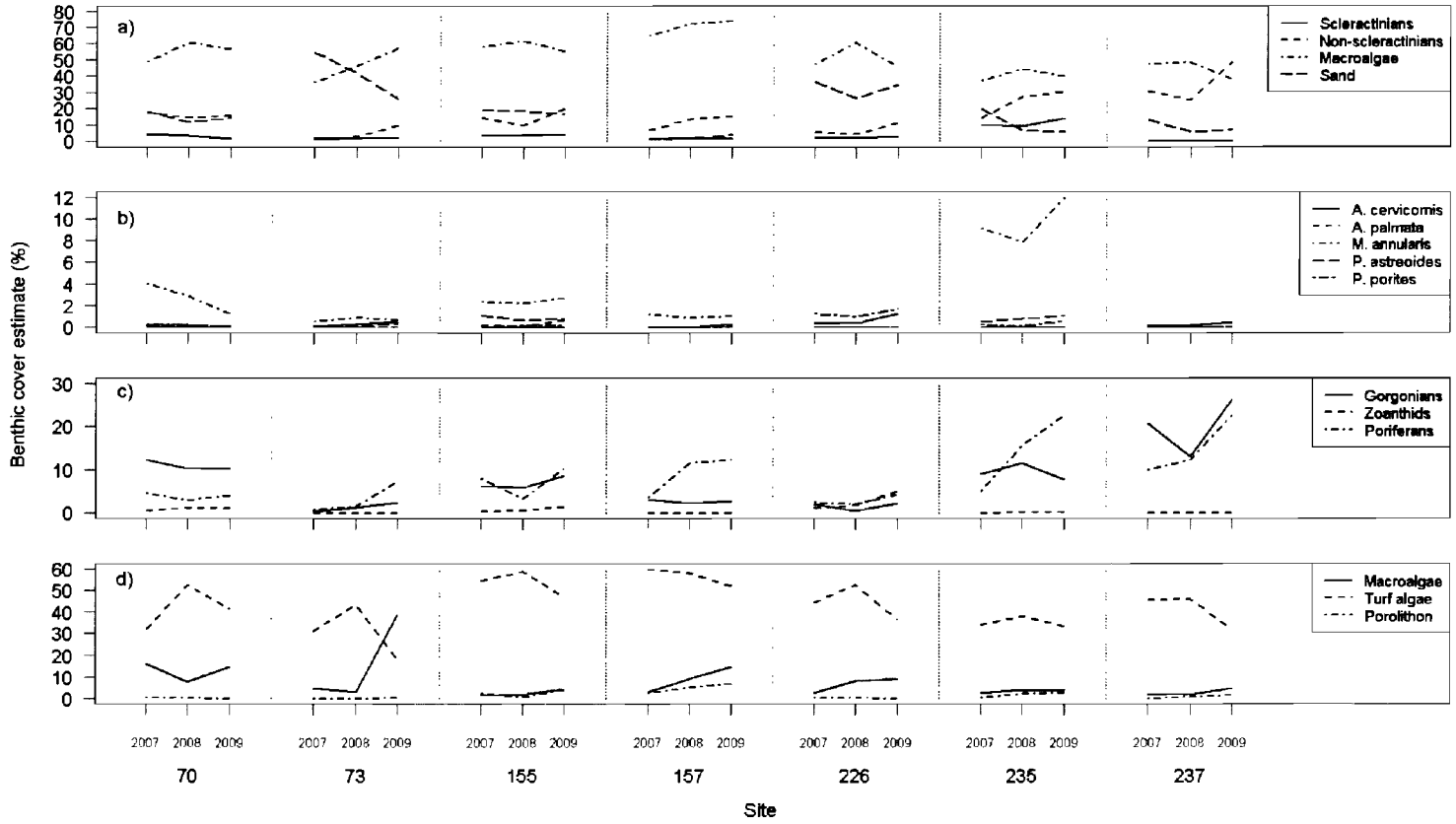

Figure 12: Benthic cover estimates for a) general classes, b) scleractinian classes, c) non-scleractinian classes, and d) algal classes. Benthic cover observed in photoquadrats collected from seven sampling sites representing different benthic communities in the back reef and reef slopes leeward of the reef crest at San Cristobal from 2007 to 2009.

Table 5: A summary of the statistical results as to whether change occurred or did not occur within select benthic cover classes at the seven sampling sites. The estimated change in benthic cover for 2007 to 2008, and the best-fit model and its associated evidence ratio are listed. Bold indicates where Model 1 (change due to year) was the best-fit model and the evidence supporting the model is 'substantial' or greater ($ER > \sqrt{10}$). The values are based on the 100 points photoquadrat^{-1} data sets with both Model 0 and Model 1 accounting for spatial autocorrelation using an exponential decay function.

Class	Transect						
	70	73	155	157	226	235	237
A. cervicornis	A	0.27%; M1: 1.33	A	A	**-0.07%; M1: >100**	A	0.01%; M0: 1.23
A. palmata	A	A	-0.03%; M1: 2.28	P	A	A	A
M. annularis	**-1.12%; M1: 26.92**	0.39%; M0: 1.14	-0.15%; M0: 2.65	-0.35%; M0: 2.54	A	-1.26%; M0: 2.33	P
P. astreoides	0.06%; M0: 2.03	**0.06%; M1: 12.17**	-0.48%; M0: 2.37	P	P	**0.34%; M1: >100**	A
P. porites	**-0.04%; M1: 8.00**	A	0.11%; M0: 2.32	A	-0.33%; M1: 1.47	-0.19%; M0: 1.82	P
Gorgonians	**-2.02%; M1: >100**	0.99%; M0: 1.95	**-0.30%; M1: >100**	-1.02%; M1: 1.09	**-1.51%; M1: >100**	**2.66%; M1: 7.70**	**-7.98%; M1: 65.16**
Zoanthids	0.60%; M0: 2.64	P	0.09%; M0: 2.16	P	0.75%; M0: 2.38	**0.13%; M1: 8.23**	P
Poriferans	**-1.54%; M1: 97.45**	**0.61%; M1: >100**	-4.76%; M1: 3.03	**8.12%; M1: >100**	-0.34%; M0: 2.70	**10.73%; M1: 8.05**	**2.33%; M1: >100**
Macroalgae	-8.42%; M1: 2.95	**-1.95%; M1: >100**	0.38%; M1: 1.04	**6.51%; M1: 56.06**	**5.55%; M1: >100**	1.20%; M0: 2.21	-0.19%; M1: 1.39
Turf algae	**20.37%; M1: >100**	**12.42%; M1: 34.15**	4.47%; M0: 1.18	-1.86%; M0: 2.38	7.83%; M0: 2.46	4.23%; M0: 2.51	0.47%; M1: 2.72
Porolithon	-0.14%; M0: 2.64	P	-1.63%; M0: 1.76	2.54%; M1: 1.14	-0.04%; M0: 1.55	**1.98%; M1: >100**	**0.59%; M1: >100**
Sand	-5.96%; M0:1.01	**-12.57%; M1: 12.48**	**-0.80%; M1: 16.81**	**0.42%; M1: 20.79**	-10.14%; M1: 1.31	-13.38%; M1: 1.97	**-7.54%; M1: 5.68**

A – Absent: Class was not observed at this location.
P – Present: Class was present at this location and had proportional benthic cover less than 0.1%.

Table 6: Same as table 5, except summarizing the statistical results for 2008 to 2009.

Class	Transect						
	70	73	155	157	226	235	237
A. cervicornis	P	**0.19%; M1: >100**	A	**0.29%; M1: 3.83**	0.88%; M0: 2.11	A	**0.35%; M1: 10.83**
A. palmata	A	A	**0.59%; M1: >100**	P	A	A	A
M. annularis	-1.63%; M0: 2.05	**-0.24%; M1: 35.04**	0.55%; M0: 2.66	0.18%; M0: 2.22	A	4.08%; M0: 2.52	A
P. astreoides	-0.12%; M0: 2.55	0.21%; M0: 1.49	0.06%; M1: 1.65	0.13%; M0: 2.20	A	0.17%; M1: 3.07	A
P. porites	-0.12%; M0: 2.49	A	**0.05%; M1: 27.93**	A	0.76%; M0: 2.69	**0.57%; M1: 3.47**	P
Gorgonians	0.12%; M0: 2.13	1.19%; M0: 1.50	**2.64%; M1: >100**	0.63%; M0: 2.22	**1.56%; M1: >100**	-4.00%; M0: 2.04	**13.28%; M1: 4.99**
Zoanthids	-0.01%; M0: 2.70	P	0.91%; M0: 1.56	P	**3.11%; M1: >100**	-0.01%; M1: 1.60	P
Poriferans	**1.03%; M1: >100**	**6.00%; M1: >100**	**6.93%; M1: >100**	0.68%; M0: 2.72	**2.27%; M1: >100**	6.94%; M0: 2.72	**10.25%; M1: >100**
Macroalgae	7.17%; M0: 1.47	**35.88%; M1: >100**	**2.29%; M1: >100**	5.44%; M0: 1.57	**0.82%; M1: 4.84**	**-0.20%; M1: >100**	**3.27%; M1: >100**
Turf algae	-10.97%; M1: 1.48	**-25.47%; M1: >100**	-11.90%; M1: 2.42	-5.94%; M0: 2.69	-16.14%; M0: 1.85	-4.70%; M0: 1.29	**-14.15%; M1: 5.02**
Porolithon	-0.18%; M0: 1.36	0.18%; M0: 2.01	3.19%; M1: 3.28	**1.90%; M1: >100**	**-0.21%; M1: 3.27**	0.29%; M0: 2.64	**0.75%; M1: >100**
Sand	2.05%; M0: 1.79	**-16.06%; M1: >100**	-1.52%; M0:1.49	**2.35%; M1: 24.65**	**8.26%; M1: 5.34**	0.37%; M1: 1.61	0.88%; M0: 1.92

A – Absent: Class was not observed at this location.
P – Present: Class was present at this location and had proportional benthic cover less than 0.1%.

Determining optimal sampling density

The sensitivity analysis demonstrated that increased point densities and increased photoquadrat totals resulted in more reliable estimates of proportional cover and more reliable detection of change. Furthermore, the four cover classes included in the sensitivity analysis (*M. annularis*, *P. astreoides*, poriferans, and sand) showed differences in the point densities and photoquadrat totals at which the proportional cover estimates for the two years (2007 and 2008) were able to be separated (Figures 13 and 14). Both *M. annularis* and *P. astreoides* required a higher point density (e.g., 50 points photoquadrat^{-1}) for proportional cover estimates between years to be separated (Figure 13) while poriferans and sand both could be separated with a lower point density (e.g., 5 points photoquadrat^{-1}; Figure 13). Similarly, *M. annularis* and *P. astreoides* required higher photoquadrat totals (e.g., 50 photoquadrats; Figure 14) for benthic cover estimates to be visually separated, and proportional cover estimates for poriferans and sand required lower photoquadrat totals (e.g., 30 photoquadrats; Figure 14).

Model selection results from the sensitivity analysis demonstrated that higher point densities and higher photoquadrat totals more reliably detected, or did not detect, change (Figures 15 and 16). Low and medium point densities failed to detect real change or may detect change when no real change occurred, whereas higher point densities result in less variance in the evidence ratios resulting in greater confidence when inferring the occurrence or lack of change (Figures 15). Similarly, low and medium photoquadrat totals may fail to detect change or detect change when no change occurred where as higher photoquadrat totals have less variance in the evidence ratios resulting in greater confidence when inferring the occurrence or lack of change (Figure 16).

In the cases of *M. annularis* and *P. astreoides*, point densities greater than or equal to 70 points photoquadrat^{-1} were required to reliably identify whether change did or did not occur (Figure 15 a and b) while photoquadrat totals greater than or equal to 40 photoquadrats were necessary for a similar result (Figure 16a and b). For *M. annularis* specifically, no change was detected in the full data set (Table 5). During the sensitivity analysis, point densities less than or equal to 10 points photoquadrat^{-1} and greater than or equal to 70 points photoquadrat^{-1} had no change detected (in this case, either an $ER < 1$,

which indicates Model 0 being selected, or $1 \leq ER < \sqrt{10}$, indicating minimal evidence for change), thereby agreeing with the results of the full data set, in 95% or more of the re-samples (Figure 15a). From point densities of 20 to 30 points photoquadrat^{-1}, the number of resamples resulting in a detection of change, which did not agree with the result of the full data set, increased from 5% to more than 25%, and then decreased to 5% as point density reached 70 points photoquadrat^{-1}. For photoquadrat totals, the percent of re-samples resulting in no change being detected increased with the number of photoquadrats (Figure 15b). At the lowest total (2 photoquadrats), less than 75% of the re-samples resulted in no change being detected, which was the result from the full data set. By 40 photoquadrats, this value had reached 95%. For *P. astreoides*, the percent of re-samples in which change was detected with substantial evidence or greater (i.e., $ER \geq \sqrt{10}$), the result of the full data set (Table 5), increased as point density increased. At point densities less than or equal to 60 points photoquadrat^{-1}, less than 50% of the re-samples resulted in a change being detected (Figure 15b). At 70 points photoquadrat^{-1}, this percentage increased to more than 50%. More than 75% of re-samples agreed with the result of the full data set at 90 points photoquadrat^{-1}. For photoquadrat totals, the percent of re-samples in which change was detected increased from less than 5% at 2 photoquadrats to just less than 75% at 50 photoquadrats (Figure 16b). For totals less than or equal to 30 photoquadrats, more than 50% of re-samples had no change detected, but for totals greater than or equal to 40 photoquadrats, change was detected in more than 50% of the re-samples.

Conversely, poriferans and sand required point densities greater than or equal to 10 points photoquadrat^{-1} (Figure 15 c and d) and photoquadrat totals greater than or equal to 20 photoquadrats (Figure 16 c and d) to reliably detect whether change did or did not occur. In poriferans, a change was detected in the full dataset (Table 5). For this class, less than 75% of the re-samples for the 5 points photoquadrat^{-1} point density resulted in change being detected with substantial evidence or greater ($ER \geq \sqrt{10}$; Figure 15c). At 10 points photoquadrat^{-1}, this percentage increased to greater than 95%, and it remained above 75% as point density increased. At totals less than or equal to 10 photoquadrats, change was detected in poriferans in less than 50% of the re-samples (Figure 16c).

However, for totals greater than or equal to 20 photoquadrats, this percentage increased to more than 50%. At 50 photoquadrats, greater than 75% of the re-samples detected change with substantial evidence or greater, while less than 5% of the resamples had Model 0 (i.e., $ER < 1$), representing no change occurred, chosen as the best-fit model (Figure 16c). Sand, which did not have change detected in the full data set (Table 5), exhibited a similar pattern of reliable results at low point densities and low photoquadrat totals. For point densities less than or equal to 5 points photoquadrat^{-1}, between 50% and 75% of re-samples did not have change detected with substantial evidence or greater having either Model 0 selected as the best-fit model (i.e., $ER < 1$) or having minimal evidence (i.e., $1 \leq ER < \sqrt{10}$) when Model 1 was selected (Figure 15d). However, this value increased to between 75% and 95% at 10 points photoquadrat^{-1}, and it was consistent as point densities increased (Figure 15d). For all photoquadrats totals, greater than 50% of re-samples did not detect change ($ER < \sqrt{10}$; Figure 16d). Less than 75% of re-samples for totals less than or equal to 10 photoquadrats did not detect change, but more than 75% of re-samples did not detect change when totals greater than or equal to 20 photoquadrats were used (Figure 16d).

In summary, low point densities (e.g., 10 points photoquadrat^{-1}) reliably detected change in poriferans and sand; however, such point densities did not reliably detect change in the two scleractinians classes. High point densities (e.g., greater than or equal to 70 points photoquadrat^{-1}) detected change in all four classes reliably. When using this methodology to detect change in rare or sparse classes, the researcher should err on the side of using a higher point densities to ensure accurate estimation of proportional cover and reliable detection of change.

During the sensitivity analysis, no distance criteria were included when points were randomly selected, and the lack of these criteria could result in the points being 'clumped' within a quadrat. This meant that points could be close to each other, and the overall point distribution could result in all of the randomly-selected points occurring within one region of the quadrat (e.g., within the top left quadrant). Occurance of such clumping could bias the results as evidence for close points is less than that of distant poins. Ideally, the spatial autocorrelation term within the models would exactly counter

this effect. To check this, I plotted the ER values for the lowest point density (i.e., 5 points photoquadrat^{-1}) with no distance criteria and with distance criteria for 1) extent of the point distribution in the x and y directions and 2) Euclidean distance between points. In both cases, all points in the photoquadrat had to be separated by greater than 2 cm. Additionally, at least one pair of points needed to met the minimum distance criterion, which varied from 2 cm to 30 cm. Figure 17 shows that inclusion of these distance criteria did not result in a different spread of ER values for *M. annularis* or sponges under either approach until the sample size was low (e.g., less than 8 re-samples). The same result was observed for *P. astreoides* and gorgonians. This confirms that there was no apparent bias and no distance criteria were required.

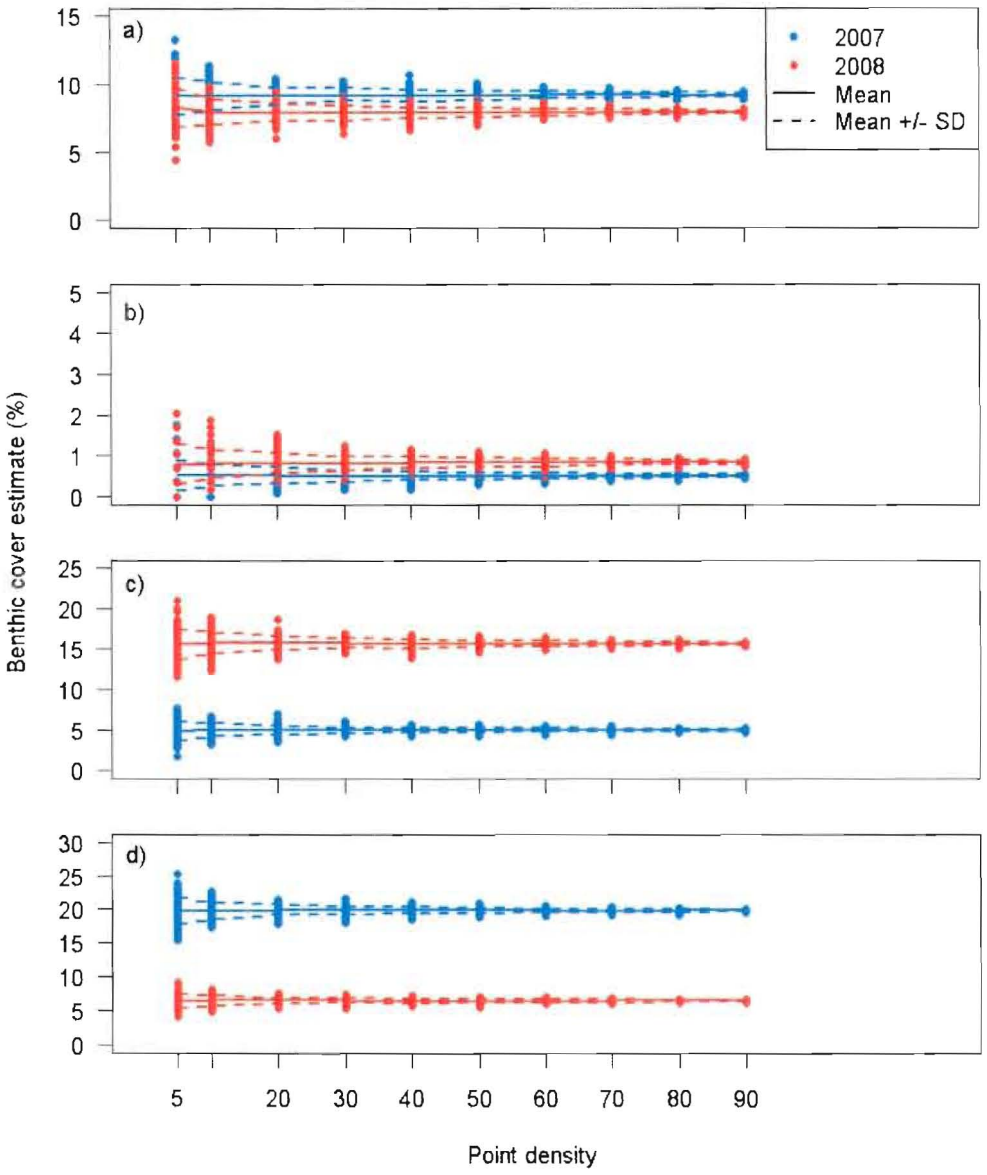

Figure 13: Effects of point density on benthic cover estimates from differing point densities for a) *M. annularis*, b) *P. astreoides*, c) poriferans, and d) sand at Site 235 for 2007 (blue) and 2008 (red), with respective totals of 57 and 59 photoquadrats, observed in 1000 random re-samples of the full data set (i.e., 100 points photoquadrat^{-1}). For each of the 10 point densities, 100 random re-samples were drawn. Each point is the estimated benthic cover from one random draw, and the means and standard deviations are with respect to the observed values for the 100 random re-samples at each point density.

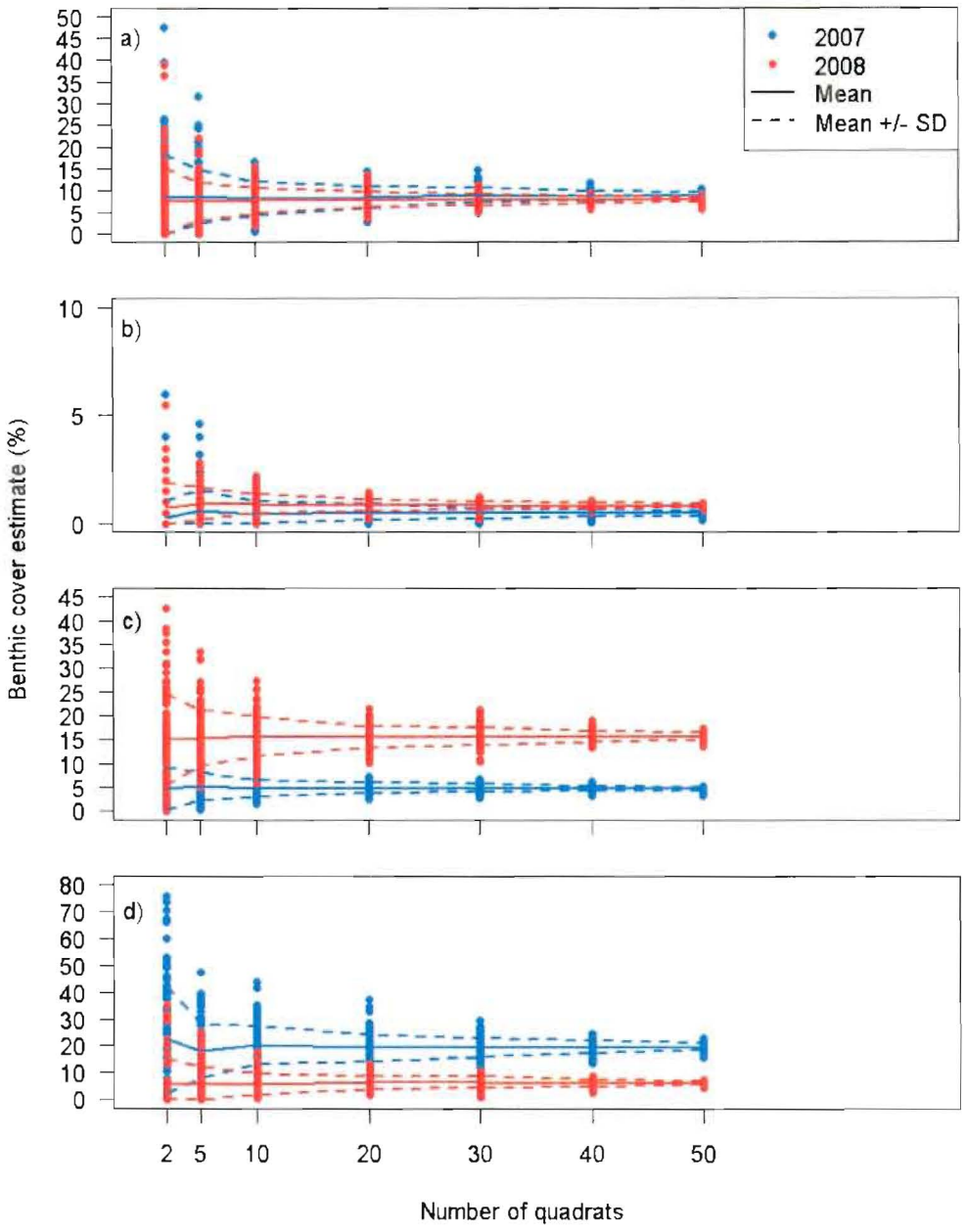

Figure 14: Similar to figure 13, but considering the effects of differing number of photoquadrats instead of the point density, on benthic cover estimates for a) *M. annularis*, b) *P. astreoides*, c) poriferans, and d) sand at Site 235 for 2007 (blue) and 2008 (red) observed in the 700 random re-samples of the full data set. Note that the y-axis scales differ between this figure and Figure 13.

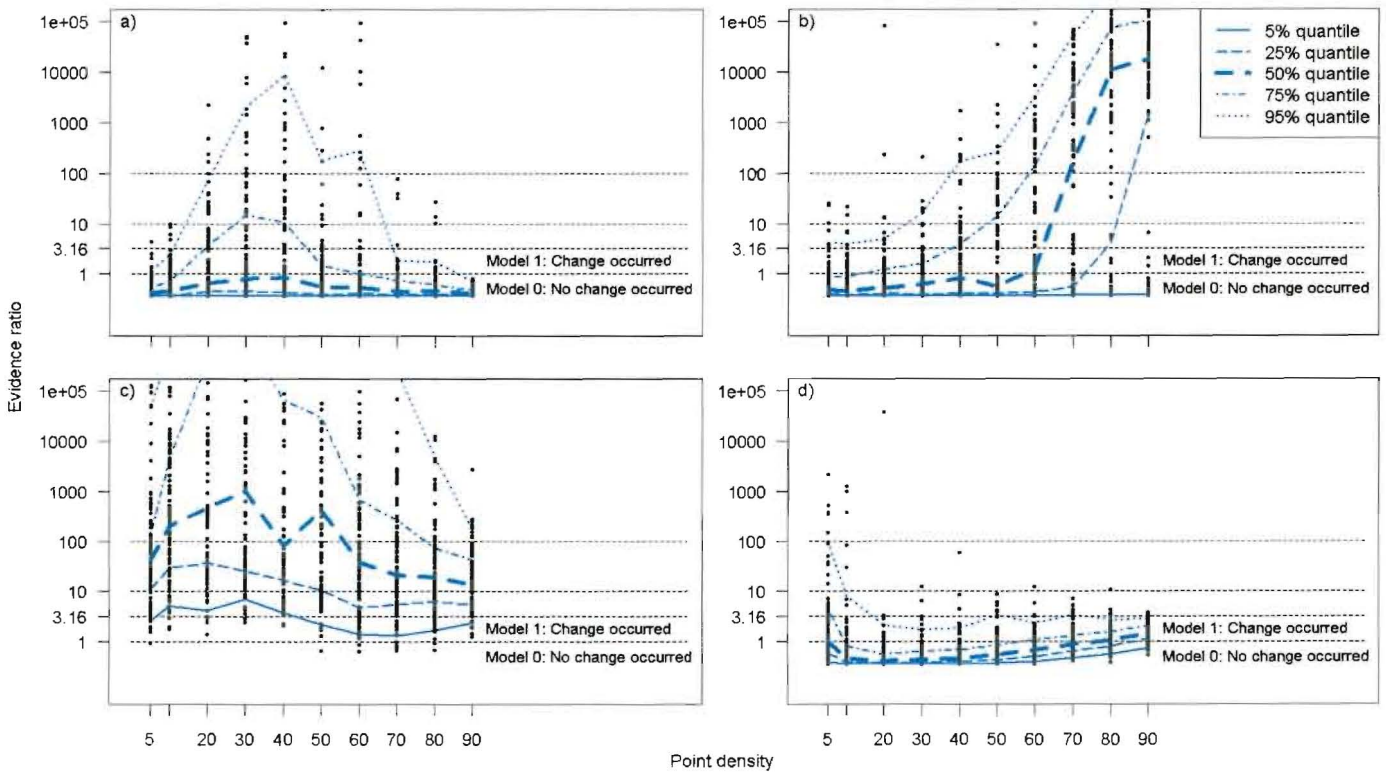

Figure 15: Evidence ratios and their 5%, 25%, 50%, 75%, and 90% quantiles from differing point densities for a) *M. annularis*, b) *P. astreoides*, c) poriferans, and d) sand for 1000 re-samples of the full data set for Site 235 in 2007 and 2008 (i.e., 100 points photoquadrat^{-1} in 116 total photoquadrats totaling 11,600 points). For each of the 10 point densities, 100 random re-samples consisting of a set of randomly selected points from each of the 57 and 59 photoquadrats for 2007 and 2008, respectively, resulting in total point counts ranging from 580 points (5 points photoquadrat^{-1}) to 10,440 points (90 points photoquadrat^{-1}). Evidence ratios greater than 1 indicate that Model 1 was the best-fit model for the re-sample, and values less than 1 indicate that Model 0 was the best-fit model.

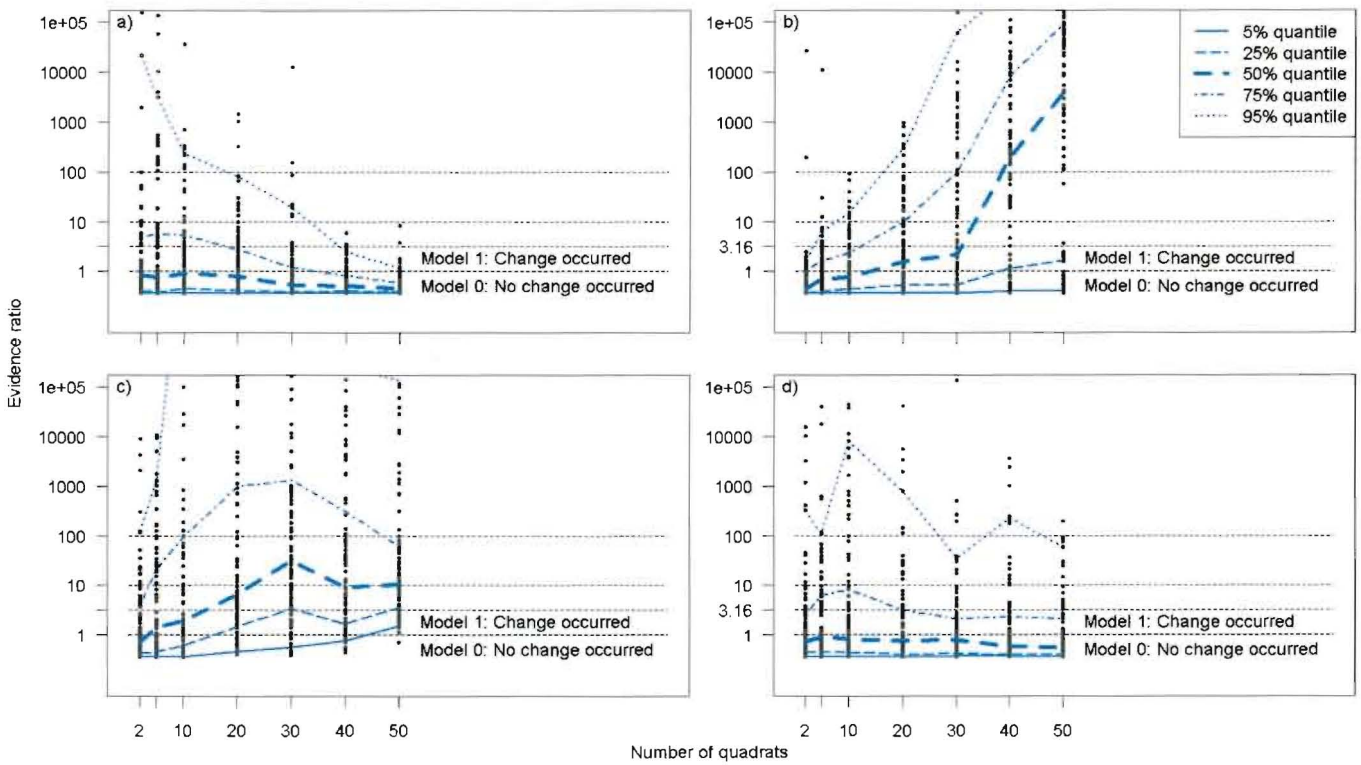

Figure 16: Same as Figure 15, but considering differing numbers of photoquadrats instead of differing point densities, for a) *M. annularis*, b) *P. astreoides*, c) poriferans, and d) sand for 700 re-samples of the full data set (i.e., 100 points photoquadrat^{-1} in 116 photoquadrats). Each re-sample consisted of a set of randomly selected photoquadrats, and all 100 points within the selected photoquadrat, from the 57 and 59 photoquadrats for Site 235 in 2007 and 2008, respectively, resulting in total point counts ranging from 200 points (2 photoquadrats) to 5000 points (50 photoquadrats).

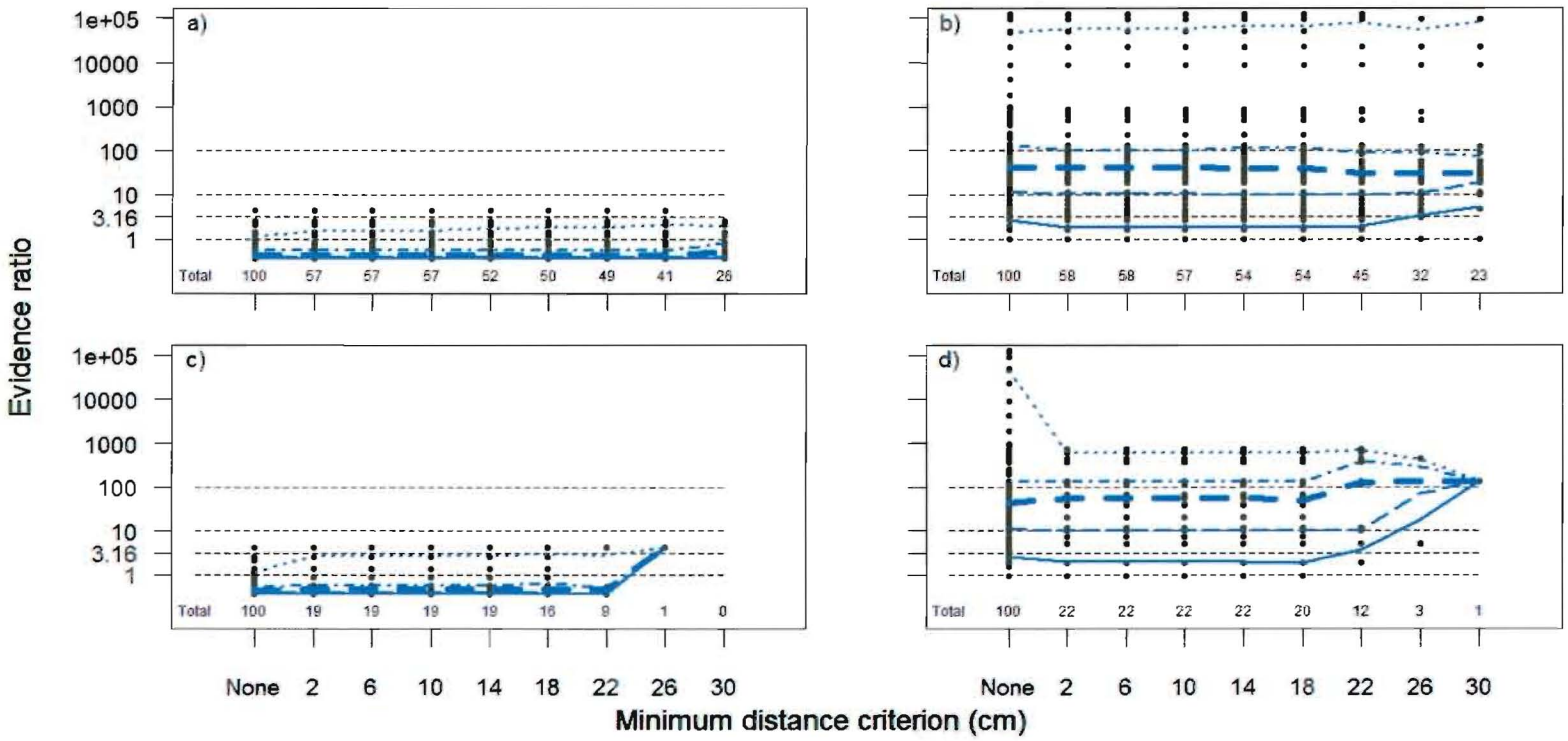

Figure 17: Evidence ratios (y-axis) supporting whether change did or did not occur as maximum distance criterion increases for *M. annularis* (a and c) and sponges (b and d) at Site 235 from 2007 to 2008. 'None' indicates no distance criterion. "Total" indicates the number of random draws which meet the given distance criteria. Two criteria were used. The first criterion required that all points within a quadrat be greater than 2 cm apart. The second criterion required that at least one pair of points within the quadrat be separated by a minimum distance. These two criteria were compared in using the x and y directions (a and b) and Euclidean distance between points (c and d).

DISCUSSION

Benthic community of San Cristobal reef

Throughout the study, the benthic community at San Cristobal reef was dominated by macroalgae and had low scleractinian cover, and non-scleractinian invertebrates had higher cover than scleractinians. These patterns were likely due to a combination of the sampling sites' locations and disturbances altering the benthic community prior to the study's beginning. The sampling sites' locations could have biased observations to low scleractinian cover and high algal cover because the sampling locations were predominantly located in the back reef zone and the transition between the back reef and reef slope. The observed communities could have also resulted from the 2005 bleaching event and passing of Hurricane Dean in 2007 meaning that communities at the reef were healthier and better developed prior to 2005. Ballantine et al. (2005) described San Cristobal reef as having overall live scleractinian cover of 18% with *Montastraea* spp. being the most abundant scleractinian and abundant *Acropora* spp. cover, including abundant *A. cervicornis* stands in the shallow areas. They further reported that *A. cervicornis* stands of La Parguera suffered near 100% mortality following the 2005 bleaching event and subsequent disease outbreak. Furthermore, numerous toppled, nearly intact structurally, dead *A. palmata* colonies were observed in 2007. Their nearly intact nature suggests that these colonies died within a short time prior to the observations, and their size suggests that significant force would have been required to topple and overturn them. It is possible that the waves generated by Hurricane Dean toppled these large *A. palmata* colonies similar to the effects of Hurricane Edith (Glynn et al. 1964). Additionally, although Site 235 had the highest scleractinian cover, the benthic community structure observed at this site was different than one would expect to find in an undisturbed community. The site contained numerous *M. annularis* colonies that provide abundant substrate for colonization by scleractinians; however, overall live *M. annularis* cover was less than 12% in 2007 and live cover of other scleractinians at this site (e.g., *P. astreoides*, *P. porites*) were also low throughout the study. The differences between the benthic communities described by Ballantine et al. (2005) and observed by this study suggest that the benthic communities underwent change from 2005 to 2007; however, this study did not quantify changes in the benthic community due

to the bleaching event, Hurricane Dean, or local-scale, chronic disturbances. Therefore, the relative contributions of sampling site placement and disturbances prior to and during the study on the observed benthic community structure cannot be separated.

At sampling Site 73, macroalgae cover dramatically increased between 2008 and 2009 due to a *Cyanobacteria* bloom. Numerous *Cyanobacteria* thalli were observed throughout the site in 2009; however, *Cyanobacteria* thalli were not observed in the photoquadrats from the same location in 2007 and 2008. In 2009, *Cyanobacteria* thalli were not observed at Site 226, but sites 70, 155, 157, 235, and 237 contain at least one photoquadrat with a "brown fuzz" that could be a *Cyanobacteria* thallus. However, this "brown fuzz" does not have the long strands observed in the *Cyanobacteria* thalli at Site 73 indicating that they could be either a different species or the same species with lesser development at Site 73. In either case, further study is required to make any conclusions regarding the causative agents and ecological changes associated with this *Cyanobacteria* bloom for this reef site.

Point density and photoquadrat total

Previous studies assessed photoquadrat methodology in comparison to other sampling methods (e.g., Bohnsack 1979; Preskitt et al. 2004; Brown et al. 2004; Luejak and Ormond 2007), assessed the effects of point density on accuracy (e.g., Carleton and Done 1995; Brown et al. 2004), assessed the effects of point density on statistical power (e.g., Brown et al. 2004; Houk and Van Woesik 2006), and assessed the effects of increasing the number of frames or photoquadrats (Brown at al. 2004; Houk and Van Woesik 2006) when sampling coral communities. The 100 points photoquadrat^{-1} density used to sample the benthic communities was greater than those used by Brown et al. (2004), Houk and Van Woesik (2006), and Carleton and Done (1995), and the photoquadrat totals of 43 to 63 photoquadrats were similar to the number of photoquadrats and frames used in those three studies. The point density used to sample the benthic communities in this study was equivalent to 400 points m^{-2}. In the sensitivity analysis, the point density ranged from five points photoquadrat^{-1} to 90 points photoquadrat^{-1}, which is equivalent to 20 points m^{-2} to 360 points m^{-2}. Carleton and Done (1995) recommended using 110 points for a 50-m^2 sample resulting in a point density of

2.2 points m^{-2}. Houk and Van Woesik (2006) compared the samples taken from 5, 10, and 15 points $frame^{-1}$ for 20, 40, and 60 frames captured from 50 m by 0.5 m (25 m^2) video transects resulting in point densities of 20, 40, and 60 points m^{-2}. Brown et al. (2004) used point densities of 10, 50, and 100 points $frame^{-1}$ with each frame covering 0.5 m^2 resulting in point densities of 20, 100, and 200 points m^{-2}. In the present study, the total number of photoquadrats per sampling location (100 m^2) in a year ranged from 43 photoquadrats to 63 photoquadrats, which is greater than those used by Carlton and Done (2006) and Brown et al. (2004) and similar to those used by Houk and Van Woesik (2006). Carleton and Done (1995) used five frames for a 50 m^2 transect, while Brown et al. (2004) used 10, 20, and 30 frames. Houk and Van Woesik (2006) used 20, 40, and 60 frames in their analysis.

Higher point densities and higher photoquadrat totals more reliably estimate benthic cover and more reliably detect change than lower point densities and lower photoquadrat totals. Additionally, the minimum point density required to detect whether change did or did not occur reliably varies with proportional cover, magnitude of change in proportional cover, and spatial autocorrelation distance (Table 7). In the sensitivity analysis, *P. astreoides*, which had less than 1% proportional cover, a change of less than 1%, and a spatial autocorrelation distance of 10 cm, required a minimum of 80 points $photoquadrat^{-1}$ for Model 1 to consistently be selected as the best-fit model with substantial evidence or greater (i.e., $ER > \sqrt{10}$). In comparison, poriferans had greater initial proportional cover (5%), a greater change in cover (11%), and greater spatial autocorrelation distance (40 cm), and thus required only five points $photoquadrat^{-1}$ for Model 1 to be selected as the best-fit model with at least 'substantial' evidence. The difference in the required minimum point densities for *P. astreoides* and poriferans was likely due to the differences in proportional cover and the changes' magnitudes. Greater spatial autocorrelation distance increased the minimum point density required for consistent model selection results; a comparison of the results for sand and poriferan demonstrates this. Sand required a higher point density (five points $photoquadrat^{-1}$) than poriferans. Both classes had similar values for proportional cover and similar magnitudes

for change; the primary difference between the two was that sand had a greater spatial autocorrelation distance (80 cm) than poriferans (40 cm).

Table 7: Summary of the minimum point densities and minimum photoquadrat totals required to detect whether change did or did not occur reliably in the four benthic cover classes included in the sensitivity analysis as identified in Figures 14 and 15.

	Proportional cover						Samples	
Class	2007	2008	Change	SACD	Best Model	ER	Pts.	Quads.
M. annularis	9.16%	7.90%	-1.26%	40	M0	2.33	50	20
P. astreoides	0.49%	0.83%	0.34%	10	M1	>100	80	30
Poriferans	4.93%	15.66%	10.73%	40	M1	8.05	2	30
Sand	19.84%	6.46%	-13.38%	80	M1	1.97	5	20

SACD – Spatial autocovariance distance (cm)
Model – Best-fit model
ER – Evidence ratio supporting the best-fit model
Pts. – Point density (points photoquadrat^{-1})
Quads. – Number of photoquadrats

The results of the present study are similar to those of previous studies; however, the recommended point densities and photoquadrat totals differed. Brown et al. (2004) evaluated the power for detecting a 10% change in benthic cover for point densities of 10, 50, and 100 points frame^{-1} for increasing numbers of frames, and they reported a higher power (i.e., a lower occurrence of Type II errors) for higher point densities and increased numbers of frames. Carleton and Done (1995) reported that digitate corals, the dominant cover class in their study with greater than 10% proportional cover, required only 40 points for precise estimates. Furthermore, the branching and massive corals, which both had approximately 5% proportional cover, required 90 and 110 points, respectively, and the rarest cover class, plating corals with approximately 1% proportional cover, required the greatest number of points (300 points). These values are lower than the values recommended by the present study. This was likely due to differences in methods for sampling and statistical analysis. The major difference between this study and previous studies was that a model-comparison approach incorporating spatial autocorrelation was used for statistical analysis instead of an ANOVA approach.

Data in ecological studies inherently contain spatial autocorrelation, which is problematic for statistical analyses due to the violation of independence between observations (Legendre and Fortin 1989; Legendre 1993; Dormann et al. 2007; Zuur et al. 2007, 2009; Kissling and Carl 2008). Previous studies did not directly address the issue of spatial autocorrelation, instead assuming that points were spatially independent. Carleton and Done (1995), Houk and Van Woesik (2006), and Luejak and Ormond (2007) acknowledged the possibility of spatial autocorrelation. Carleton and Done (1995) used fewer points per frame to avoid autocorrelation. Luejak and Ormond (2007) remarked that uniformly spaced, non-random points could result in autocorrelation, and they used randomly placed points instead. Houk and Van Woesik (2006) acknowledged that increasing the number of points per frame (i.e., point density), "will eventually result in autocorrelation." These three studies assumed that the distance between points within frames was sufficient to assume independence between observations within frames. They also implicitly assumed that points in different frames were spatially independent. Based on these two assumptions, these authors proceeded to use analysis of variance (ANOVA) to detect change and performed power analyses to determine appropriate sample sizes. The present study demonstrated that spatial autocorrelation can occur in point densities from 5 points photoquadrat^{-1} (i.e., 20 points m^{-2}) to 100 points photoquadrat^{-1} (i.e., 400 points m^{-2}), which are equivalent to or greater than those used by Houk and Van Woesik (2006) and Brown et al. (2004), thereby violating the assumption of independence between observations. Only Carleton and Done (1995) used point densities lower than those of the sensitivity analysis. The methods developed herein successfully accounted for spatial autocorrelation, as evidenced by reduced spatial autocorrelation within the model residuals, and they serve as an example of how to address spatial autocorrelation within point data.

Implications for Long-Term Monitoring of Coral Reefs

Two coral reef monitoring programs that sample benthic communities using points overlaid on digital photographs or digital video transects are the Coral Reef Evaluation and Monitoring Project (CREMP) and the Hawaii Coral Reef Assessment and Monitoring Program (CRAMP). CREMP collected video transects of the reef benthos for

sampling sites within the Florida Keys National Marine Sanctuary (FKNMS) and Dry Tortugas Ecological Reserve from which estimate proportional benthic cover is estimated (Jaap et al. 2000; Maliao et al. 2008). Up to 1999, the monitoring program selected 60 abutting still-frames from each video transect creating a 40 cm by 20 m belt transect covering approximately 8 m^2. Ten points were overlaid on each of the 60 frames resulting in 600 points per belt transect and an approximate point density of 75 points m^{-2}. CRAMP collected digital video along a 10-m transect and selected 20 frames from each transect placing 50 points over each frame to monitor sites in Hawaii (CRAMP 2008). In 2003, the program shifted to using images collected with digital cameras providing 20 images, each covering a 50-cm by 69-cm (0.345 m^2) area, per 10-m transect, and placing 50 randomly placed points over each image resulting in a point density of approximately 145 points m^{-2}. In comparison, the sensitivity analysis demonstrated that either 70 points photoquadrat^{-1} (280 points m^{-2}) or 10 points photoquadrat^{-1} (40 points m^{-2}) and either 40 photoquadrats or 20 photoquadrats were required depending on the proportional benthic cover of the tested class and the difference between estimates to be detected.

Based on the results of the present study, the point densities and photoquadrat totals used by CREMP and CRAMP are likely sufficient for reliably estimating proportional cover for benthic cover classes with high cover and for detecting large changes. However, the point densities used by both monitoring programs are insufficient for either accurately estimating proportional cover for classes with low proportional cover or detecting small changes in proportional cover. Furthermore, the present study demonstrated that the photoquadrat totals used by both CREMP and CRAMP are sufficient for detecting large changes. Estimated proportional benthic cover for scleractinians for some of the monitoring sites established by CREMP and CRAMP was less than estimated proportional cover for *M. annularis* at site 235 in 2007 and 2008 (11%). Maliao et al. (2008) described a phase-shift in the benthic communities of the FKNMS based on CREMP data, and they noted that mean estimated cover for all scleractinians combined and *M. annularis* were less than 10% and 2%, respectively, from 1996 to 2000. In Maui, mean proportional cover for scleractinians decreased at five sites, increased at one site, and was consistent for three sites from 1995 to 2005. Of these nine sites, four had less than 15% proportional benthic cover for scleractinians in 2005. Due to

these low proportional benthic cover estimates for scleractinians, it is recommended that both CREMP and CRAMP increase the point densities used in their monitoring programs.

Point densities similar to those used by CREMP and CRAMP were found to contain predictable patterns of spatial autocorrelation between the points, which violates the assumption of independence between points meaning that the statistical analyses for detecting change may lead to spurious inferences regarding change over time for benthic cover classes if the analyst doe not account for spatial autocorrelation between points. It is recommended that CREMP and CRAMP address spatial autocorrelation within their data sets to reduce the occurrence of spurious inferences. The approach of incorporating a spatial autocorrelation term into a model-comparison approach developed in this study provides a statistical method for detecting change that accounts for spatial autocorrelation and will provide more reliable results.

Declines in the health of coral reef ecosystems around the world due to the synergistic effects of natural and anthropogenic disturbances will result in the loss of goods and services humans derive from these ecosystems. A common practice in monitoring reef health is the collection of digital images and video and estimation on proportional benthic cover of benthic community members, with particular focus on live scleractinian cover, using points randomly placed over images or video. While this method is effective for estimating proportional benthic cover and detecting change over time, this study demonstrated that the methodology needs to be improved to increase reliability of benthic cover estimates and reliability of change detection. Recommended improvements include increasing point densities, increasing photoquadrat totals, and accounting for spatial autocorrelation between observations. Implementing these improvements will provide better characterization of benthic community structure and fewer false inferences of change in benthic cover improving the advice researchers using this methodology provide to decision-makers regarding policy actions.

REFERENCES

Akaike H. 1973. Information theory as an extension of the maximum likelihood principle. In: Second International Symposium on Information Theory. BN Petrov and F Csaki (Eds.). Akademiai, Budapest.

Augustine NH, Mugglestone MA, and Buckland ST. 1996. An autologistic model for the spatial distribution of wildlife. Journal of Applied Ecology. 33:339-347

Baker VJ, Bass DK, Christie CA, Johnson DB, Miller IR, Miller-Smith BA, Moran PJ, Thompson AA. 1990. Manta tow surveys of the Great Barrier Reef. Coral Reefs. 9(3):104.

Ballantine DL, Appledoorn RS, Yoshioka P, Weil E, Armstrong R, Garcia JR, Otero E, Pagan F, Sherman C, Hernandez-Delgado EA, Bruckner A, Lilyestrom C. 2008. Biology and ecology of Puerto Rican coral reefs. In: Coral reefs of the USA. BM Riegl and RE Dodge (Eds). Berlin: Springer Science and Business Media.

Bohnsack JA. 1979. Photographic quantitative sampling of hard-bottom benthic communities. Bulletin of Marine Science. 29(2): 242-252.

Bries JM, Debrot AO, Meyer DL. 2004. Damage to the leeward reefs of Curacao and Bonaire, Netherlands Antilles from a rare storm event: Hurricane Lenny, November 1999. Coral Reefs 23(2):297-307.

Brown E, Cox E, Jokiel P, Rodgers K, Smith W, Tissot B, Coles SL, Hultquist J. 2004. Development of benthic sampling methods for the Coral Reef Assessment and Monitoring Program (CRAMP) in Hawai'i. Pacific Science. 58(2):145-158.

Burnham KP and Anderson DR. 2002. Model selection and multimodel inference. Second edition. Springer-Verlag. New York.

Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill R, Paruelo J, Raskin R, Sutton P, van den Belt M. 1997. The value of the world's ecosystem services and natural capital. Nature. 387:253-260

[CRAMP] Hawaiian Coral Reef Assessment and Monitoring Program. [2008]. CRAMP Methods. [Internet]. [cited 2010 September 09]. Available from: http://cramp.wcc.hawaii.edu/LT_Montoring_files/lt_methods.htm

Croyle Z. 2009. Analysis of baseflow trends related to upland groundwater pumping for Las Garzas, San Clemente, Potrero, and San Jose creeks. [MSc thesis]. Seaside (CA): California State University Monterey Bay. 116 p. Available from: http://sep.csumb.edu/cwsp/theses/Croyle_Thesis_090422.pdf

DeVantier LM, De'ath G, Turak E, Done TJ, Fabricius KE. 2006. Species richness and community structure of reef-building corals on the nearshore Great Barrier Reef. Coral Reefs. 25(3):329-340.

Done TJ, Turak E, Wakeford M, DeVantier L, McDonald A, Fisk D. 2007. Decadal changes in turbid-water communities at Pandora reef: loss of resilience or too soon to tell? Coral Reefs. 26(4):789-805.

Donner SD, Knutson TR, Oppenheimer. 2007. Model-based assessment of the role of human-induced climate change in the 2005 Caribbean coral bleaching event. Proceedings of the National Academy of Science. 104(13):5483-5488.

Dormann CF, McPherson JM, Araújo MB, Bivand R, Bollinger J, Carl G, Davies RG, Hirzel A, Jetz W, Kissling WD, Kühn I, Ohlemüller R, Peres-Neto PR, Reineking B, Schröder B, Schurr FM, Wilson R. 2007. Methods to account for spatial aurocorrelation in the analysis of species distributional data: a review. Ecography. 30: 609-628.

ERDAS. 2009. ERDAS Product Information: ERDAS IMAGINE. [Internet] [cited 2009 December 21] Available from: http://www.erdas.com/tabid/84/currentid/1050/default.aspx

Faure G. 1989. Degradation of coral reefs at Moorea Island (French Polynesia) by *Acanthaster planci*. Journal of Coastal Research. 5(2):295-305.

Fitt WK, Spero HJ, Halas J, White MW, Porter JW. 1993. Recovery of the coral *Montastraea* annularis in the Florida Keys after the 1987 Caribbean "bleaching" event. Coral Reefs 12(1):57-64.

Franklin JL. 2008. Tropical Cyclone Report: Hurricane Dean (AL042007) (Revised 47 April 2008). [Internet]. [cited 2010 February 25]. Available from: www.nhc.noaa.gov/pdf/TCR-AL042007_Dean.pdf

Garcia-Sais J, Appeldoorn R, Bruckner A, Caldow C, Christensen JD, Lilyestrom C, Monaco ME, Sabater J, Williams E, Diaz E. 2005. The state of coral reef ecosystems of the Commonwealth of Puerto Rico. In: The state of coral reef ecosystems of the United States and Pacific Freely Associated states. 2005. NOAA Technical memorandum NOS NCCOS 11. NOAA/NCCOS Center for Coastal Monitoring and Assessment's Biogeography Team. Silver Spring, MD.

Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR. 2003. Long-term region-wide decline in Caribbean corals. Science 301(5635):958-960.

Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR. 2005. Hurricanes and Caribbean coral reefs: impacts, recovery patterns, and role in long-term decline. Ecology 86(1):174-184.

Garmin. 2009. GPSMAP 76CSx. [Internet] [cited 2009 December 21] Available from: https://buy.garmin.com/shop/shop.do?cID=161&pID=351

Glynn PW, Almodovar LR, Gonzalez JG. 1964. Effects of Hurricane Edith on marine life in La Parguera, Puerto Rico. Caribbean Journal of Science. 4:335-345.

Guild L, Armstrong R, Goodman J, Lobitz B. 2006. Coral Reef Bleaching and Threats to Biodiversity in Puerto Rico. NASA Research Proposal. NRA NNH06ZZDA001N-IDS ROSES-2006. A.14 Interdisciplinary Research in Earth Science Subelement 3: Biodiversity and Disturbance.

Guild L, Lobitz B, Armstrong R, Gilbes F, Goodman J, Detres Y, Berthold R, Kerr J. 2008. NASA airborne AVIRIS and DCS remote sensing of coral reefs. Proceedings of the 11th International Coral Reef Symposium. Ft. Lauderdale, Florida. 7-11 July 2008. Session number 17.

Haas A, el-Zibdah M, Wild C. 2010. Seasonal monitoring of coral-algae interactions in fringing reefs of the Gulf of Aqaba, Northern Red Sea. Coral Reefs. 29(1):93-103.

Hill J and Wilkinson C. 2004. Methods for ecological monitoring of coral reefs. Australian Institute of Marine Science. Townsville, Queensland.

Houk P and Van Woesik R. 2006. Coral reef benthic video surveys facilitate long-term monitoring in the Commonwealth of the Northern Mariana Islands: Towards an optimal sampling strategy. Pacific Science. 60(2):177-189.

Hudson JH, Hanson KJ, Halley RB, Kindinger JL. 1994. Environmental implications of growth changes in *Montastraea annularis*: Biscayne National Park, Florida. Bulletin of Marine Science. 54(3):647-669.

Hughes TP. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science. 265(5178):1547-1551

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas JA, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301(5635):929-933.

Humann P and DeLoach N. 2002. Reef Coral Identification. Second. Jacksonville: New World Publications, Inc.

Jaap WC, Porter JW, Wheaton J, Hackett K, Lybolt M, Callahan MK, Tsokos C, Yanev G. 2001. EPA/FKNMS Coral reef monitoring project updated executive summary. 1996-2000. [Internet] [cited 2010 September 06] Available from: http://ocean.floridamarine.org/fknms_wqpp/products/cremp/reports/annrpt00.pdf

Japp WC and McField MD. 2001. Video sampling for monitoring coral reef benthos. Bulletin of the Biological Society of Washington. 10:269-273.

Kissling WD and Carl G. 2008. Spatial autocorrelation and the selection of simultaneous autoregressive models. Global Ecology and Biogeography. 17(1):59-71.

Kohler KE and Gill SM. 2006. Coral Point Count with Excel extensions (CPCe): A Visual Basic program for determination of coral and substrate coverage using random point count methodology. Computers and Geosciences. 32(9):1259-1269

Kühn I. 2007. Incorporating spatial autocorrelation may invert observed patterns. Diversity and Distributions. 13:66-69.

Legendre P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology. 74(6):1659-1673.

Legendre P and Fortin M. 1989. Spatial pattern and ecological analysis. Vegetatio. 80(2):107-138.

Legendre P, Dale MRT, Fortin M, Gurevitch J, Hohn M, Myers D. 2002. The consequences of spatial structure for the design and analysis of ecological surveys. Ecography 25(5):601-615

Lessios HA, Robertson DR, Cubit JD. 1984. Spread of *Diadema* mass mortality through the Caribbean. Science. 226(4672):335-337.

Lobitz B, Guild L, Armstrong R, Montes M, Goodman J. 2008. Pre-preprocessing 2005 AVIRIS data for coral reef analysis. Proceedings of the 11th International Coral Reef Symposium. Ft. Lauderdale, Florida. 7-11 July 2008. Session number 17.

Luejak W and Ormond RFG. 2007. Comparative accuracy and efficiency of six coral community survey methods. Journal of Experimental Marine Biology. 351:168-167.

Maliao RJ, Turingan RG, Lin J. 2008. Phase-shift in coral reef communities in the Florida Keys National Marine Sanctuary (FKNMS), USA. Marine Biology. 154:841-853.

Miller J, Waara R, Muller E, Rogers CS. 2006. Coral bleaching and disease combine to cause extensive mortality on reefs in the U.S. Virgin Islands. Coral Reefs. 25(3):418

Moberg F and Folke C. 1999. Ecological goods and services of coral reef ecosystems. Ecological Economics. 29(2):215-233.

Muller EM, Rogers CS, Spitzack AS, van Woesik R. 2008. Bleaching increases likelihood of disease on *Acropora palmata* in Hawksnest Bay, St. John, US Virgin Islands. Coral Reefs 27(1):191-195.

[NOAA] National Oceanographic and Atmospheric Administration. 2006. Endangered and Threatened Species: Final Listing Determinations for Elkhorn and Staghorn Coral. [Internet]. [cited 2009 December 15]. Available from: http://www.nmfs.noaa.gov/pr/pdfs/fr/fr71-26852.pdf

[NOAA] National Oceanographic and Atmospheric Administration. 2008. Endangered and Threatened Species; Critical Habitat for Threatened Elkhorn and Staghorn Corals; Final Rule. [Internet]. [cited 2009 December 15]. Available from: http://www.nmfs.noaa.gov/pr/pdfs/fr/fr73-72210.pdf

[NOAA] National Oceanographic and Atmospheric Administration. 2010. Endangered and Threatened Wildlife; Notice of 90-Day Finding on a Petition to list 83 Species of Corals as Threatened or Endangered Under the Endangered Species Act. [Internet]. [cited 2010 February 25]. Available from: http://sero.nmfs.noaa.gov/pr/esa/pdf/75FR6616_90day_Finding_83_Corals.pdf

Oxenford HA, Roach R, Brathwaite A, Nurse L, Goodridge R, Hinds F, Baldwin K, Finney C. 2008. Quantitative observations of a major coral bleaching event in Barbados, Southeastern Caribbean. Climatic Change. 87(3-4):435-449.

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredas G, Warner RR, Jackson JBC. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science. 301(5635):955-958.

Preskitt LB, Vroom PS, Smith CM. 2004. A rapid ecological assessment (REA) quantitative survey method for benthic algae using photoquadrats with scuba. Pacific Science. 58(2):201-209.

R Development Core Team. 2009. R: A language and environment for statistical computing. Vienna, Austria. R Foundation for Statistical Computing.

Rowlands GP, Purkis SJ, Riegl BM. 2008. The 2005 coral-bleaching event Roatan (Honduras): Use of Psuedo-invariants features in satellite assessments. 53(1):99-112.

Ryan KE, Walsh JP, Corbett DR, Winter A. A record of recent change in terrestrial sedimentation in a coral-reef environment, La Parguera, Puerto Rico: A response to coastal development. Marine Pollution Bulletin. 56(6):1177-1183.

Spectra Vista Corporation. 2010. [Internet] [cited 2010 May 4] Available from: http://www.spectravista.com/1500.html

Steiner SCC and Kerr JM. 2008. Stony corals in Dominica during the 2005 bleaching episode and one year later. In: Revista de Biologia Tropical, 56 (Supl. 1): International Journal of Tropical Biology. U.S. Virgin Islands: Association of Marine Laboratories of the Caribbean.

Stimson J, Sakai K, Sembali H. 2002. Interspecific comparison of the symbiotic relationship in corals with high and low rates of bleaching-induced mortality. Coral Reefs 21(4):409-421.

Suzuki A, Gagan MK, Fabricius KE, Yukino I, Kawahata H. 2003. Skeletal isotope microprofiles of growth perturbations in *Porites* colonies during the 1997-1998 mass bleaching event. Coral Reefs 22(4):357-369.

Szmant AM. 2002. Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline. Estuaries and Coasts. 25(4):743-766.

Veron JEN. 2000a. Corals of the World. Vol. 1. 3 vols. Townsville, Australia: Australian Institute of Marine Science and CCR Qly Pty Ltd.

Veron JEN. 2000b. Corals of the World. Vol. 2. 3 vols. Townsville, Australia: Australian Institute of Marine Science and CCR Qly Pty Ltd.

Veron JEN. 2000c. Corals of the World. Vol. 3. 3 vols. Townsville, Australia: Australian Institute of Marine Science and CCR Qly Pty Ltd.

Whelan KRT, Miller J, Sanchez O, Patterson M. 2007. Impact of the 2005 coral bleaching event on *Porites porites* and *Colpophyllia natans* at Tektite Reef, US Virgin Islands. Coral Reefs. 26(3):689-693.

Wilkinson C. 2000. Status of coral reefs of the world: 2000. Townsville, Queensland. Australian Institute of Marine Science.

Wilkinson C. 2008. Status of coral reefs of the world: 2008. Townsville, Queensland. Global Coral Reef Monitoring Network.

Wilkinson C and Souter D. 2008. Status of Caribbean corals reefs after bleaching and hurricanes in 2005. Townsville, Australia: Global Coral Reef Monitoring Network, and Reef and Rainforest Centre.

Winter A, Appeldorn RS, Bruckner A, Williams, Jr. EH, Goenaga C. 1998. Sea-surface temperatures and coral bleaching off La Parguera, Puerto Rico. Coral Reefs 17(4):377-382.

Zuur AF, Ieno EN, Smith GM. 2007. Analyzing ecological data. Springer Science+Bussiness Media. New York, New York.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R. Springer Science+Bussiness Media. New York, New York.

CONSERVATION AND REMOTE SENSING OF CORALS REEFS

Context for this study

In 2005, anomalously high sea surface temperatures were observed in the western Atlantic Ocean and northeastern Caribbean Sea persisting for 4 to 6 months (Donner et al. 2008; Wilkinson and Souter 2008). The prolonged exposure to elevated sea surface temperatures resulted in large-scale bleaching of scleractinians in reefs throughout the Caribbean (Miller et al. 2006; Donner et al. 2007; Whelan et al. 2007; Oxenford et al. 2008; Muller et al. 2008; Rowlands et al. 2008; Steiner and Kerr 2008; Wilkinson and Souter 2008). In Puerto Rico, 52 scleractinian species bleached, and disease outbreaks followed the bleaching event (Ballantine et al. 2008). Due to the massive scale of the bleaching event, the US Coral Reef Task Force mobilized researchers from the National Oceanographic and Atmospheric Administration (NOAA), the National Park Service (NPS), and the National Aeronautics and Space Administration (NASA) to collect data on the extent and impact of the bleaching event on Caribbean reefs within U.S. jurisdictions (Guild et al. 2006, 2009). The NASA researchers collected hyperspectral imagery to map study locations in La Parguera, Puerto Rico, and St. John and St. Croix, U.S. Virgin Islands (Guild et al. 2006, 2009). In 2006, Dr. Liane Guild of NASA Ames Research Center and collaborators from the University of Puerto Rico Mayaguez received funding from NASA to process the 2005 Advanced Visible/Infrared Imaging Spectrometer (AVIRIS) imagery using a linear spectral unmixing model (Guild et al. 2006).

Dr. Guild and her collaborators aimed to measure change in the patch reefs in La Parguera, Puerto Rico, using a combination of airborne-hyperspectral imagery and field-based data (Guild et al. 2006, 2009). The airborne-hyperspectral data were collected using AVIRIS, an airborne sensor developed by NASA's Jet Propulsion Laboratory that first went into service in 1987 (Vane et al. 1993; NASA JPL 2009). The sensor has 224 contiguous spectral bands from 400 to 2500 nm with a spectral resolution (i.e., width of each spectral band or channel) of ~10 nm (Vane et al. 1993; Richards and Jia 2006). This resolution gives the sensor ~31 contiguous bands in the visible spectrum (400 nm to 700nm) (Richards and Jia 2006), where coral reef benthic have peaks in their spectral

signatures (Lubin et al. 2001; Hochberg et al. 2004; Guild et al. 2009; Lobitz et al. 2009). The spatial resolution (i.e., pixel size) of AVIRIS data depends on the altitude of the aircraft on which it is mounted (Vane et al. 1993; NASA JPL 2009). For instance, the sensor has been flown on-board the ER-2 jet and Twin Otter turboprop providing spatial resolutions of ~17 m and ~4 m, respectively (NASA JPL 2009). During the 2005 flight in Puerto Rico, AVIRIS was mounted on NOAA's Twin Otter aircraft resulting in a spatial resolution of ~4m for the hyperspectral imagery (Guild et al. 2009).

As part of the NASA funded project, the researchers collected ground truth data to validate the interpretation of the hyperspectral imagery and to track change in the benthic community at San Cristobal and Media Luna patch reefs in La Parguera, Puerto Rico (Guild et al. 2006). The ground truth data consisted of end-member spectra for dominant benthic cover classes (e.g., scleractinians, algae, sand) collected using the GER 1500 spectrometer (Spectra Vista Corporation 2010) to train the spectral unmixing model. Photoquadrats (i.e., underwater pictures of quadrats) were collected to provide benthic cover estimates of coral, macroalgae, and sand at the study sites in from 2007 to 2009 and to provide independent verification of the spectral unmixing model results.

The present study grew out of the NASA-funded work. Changes in proportional benthic cover estimates for invertebrates, algae, and sand derived from the photoquadrats needed to be assessed accurately and in a manner that could provide information for the classification of the hyperspectral imagery. To meet this need, the approach described in the 'Journal Article' was developed and evaluated. The following sections provide background on the current state of both coral reef ecosystems and coral reef conservation. The background is not extensive, as such, an effort was beyond the scope of this project. Despite this, a reader unfamiliar with the topics of coral reef ecology and coral reef conservation should gain a better understanding of the plight of these marine ecosystems and the steps being taken to conserve them for current and future generations.

The need for coral reef conservation

Coral reef ecosystems provide natural, economic, social, and cultural benefits (Jackson 1997; Moberg and Folke 1999; Hughes et al. 2003); however, natural and anthropogenic disturbances synergistically degrade coral reef ecosystems and threaten

their continued existence (Hughes 1994; Gardner et al. 2003; Pandolfi et al. 2003). Coral reefs are rigid wave-resistant frameworks occurring in tropical regions between 30' N and 30' S (Veron 2000) formed through biological accretion of aragonite (Wood 1999), a form of calcium carbonate ($CaCO_3$), and deposition and solidification of sediments (Schlager 2005). Costanza (1997) estimated that coral reefs ecosystems provided $375 billion in ecosystem goods and services on a global scale; however, Wilkinson (2008) estimated 19% of reefs are lost (i.e., not functional), 15% are seriously threatened with loss in the next 10 to 20 years, and 20% are under threat of loss in the next 20 to 40 years. Given recent declines in coral reef ecosystems and predicted decreases in the near future due to changing climate, it is no surprise that Hughes et al. (2003) claim, "There are no pristine reefs left."

Natural and anthropogenic disturbances have synergistically degraded coral reefs and compromised coral reef ecosystem resilience. Natural disturbances include hurricanes (Bythell at al 1993; Hughes 1994; Bries et al. 2004; Gardner at al 2005), crow-of-thorns seastar outbreaks (Faure 1989), disease outbreaks (Lessios et al. 1984; Hughes 1994; Muller et al. 2008; Raymundo et al. 2008), bleaching events (Lasker et al. 1984; Lesser et al. 1990), invasive species (Fenner and Banks 2004), and changing ocean chemistry (Kleypas et al. 1999; Kleypas and Langdon 2006; Hoegh-Guldberg et al. 2007). Anthropogenic disturbances include destructive fishing practices (Jackson 1997; Fox and Caldwell 2006), coral mining (Dulvy et al. 1995; Rajasuriya et al. 1995; Semesi et al. 1998), over-fishing (Hughes 1994; Sebens 1994; Jackson et al. 2001), trampling during recreational activities (Hawkins and Roberts 1993), and nutrient enrichment (Szmant 2002). These natural and anthropogenic disturbances have been implicated in past declines in coral reef health (Hughes 1994; Gardner et al. 2003) and are predicted to contribute to future declines as well (Hughes et al. 2003; Donner et al. 2005). Further, scientists predict global climate change will further degrade coral reef ecosystem health and undermine resilience (Hughes et al. 2003; Hoegh-Guldberg et al. 2007).

Scientists predict increases in atmospheric carbon dioxide (CO_2) and other green house gases due to human activities will alter global climate and oceanographic patterns (Karl and Trenberth 2003). The changes associated with these global changes potentially threaten to alter ecological processes, particularly disturbance regimes, within coral reef

ecosystems by increasing ocean acidity (i.e., ocean acidification) (Kleypas et al. 1999; Kleypas and Langdon 2006; Hoegh-Guldberg et al. 2007) and increasing sea surface temperatures (Hughes et al. 2003; Simpson et al. 2009) leading to increased intensity and frequency of bleaching events (Donner et al. 2005; McWilliams et al. 2005; Done and Jones 2006), disease outbreaks (Bruno et al. 2007; Muller et al. 2008), and hurricanes (Hughes et al. 2003). Beyond the individual effects associated with ocean acidification, hurricanes, and elevated sea surface, these disturbances can act synergistically thereby increasing their effects (Sebens 1994). Of particular concern regarding the future of coral reef ecosystems under altered global conditions is the increase in episodes of elevated water temperatures persisting for extended periods.

Bleaching is a stress response exhibited by scleractinians, gorgonians, hydrocorals, zoanthids, and sponges in which the host expels its endosymbiotic algae, called zooxanthellae (*Symbiodinium* spp.), or the zooxanthellae lose their ability to photosynthesize (Lasker et al. 1984; Vicente 1990; Fitt et al. 2001). This stress response occurs in response to thermal stress (Causey et al. 1988; Cook et al. 1989; Gates 1990), changes in salinity (Goreau 1964), increased ultraviolet light exposure (Lesser et al. 1990; Brown et al. 2002; Lesser and Farrell 2004), and oxidative stress (Lesser et al. 1990; Lesser 1997; Finelli et al. 2006). It has been documented in nearly all major coral reef regions (Cook et al. 1990; Hayes and Bush 1990; Glynn 1993; Winter et al. 1998; Smith 2001; Barton and Casey 2005; Golbuu et al. 2007). The loss or reduction of photosynthesis by zooxanathellae reduces the amount of energy the algae provide to their hosts, and this loss of energy can have lasting impacts on the health of the host. However, the scale and impact of bleaching differs among scleractinians and reef depending on location, zooxanthellate clade, and previous exposure to thermal stress (Gates 1990; Gleason 1993; Berkelmans and Oliver 1999; Marshall and Baird 2000; Stimson et al. 2002; Brown et al. 2002; Riegl 2003; D'Croz and Mate 2004; Golbuu et al. 2007) suggesting that some regions or reef may be more resilient to environmental stressors that lead to bleaching. Bleaching in scleractinians reduces aragonite deposition rates (Goreau and Macfarlane 1990; Leder et al. 1991; Suzuki et al. 2003), increases susceptibility to diseases (Muller et al. 2008), impairs reproduction (Szmant and Gassman 1990), and causes mortality (Whelan at al 2007). In mild cases, these effects do not have lasting

impacts on the benthic community composition because the affected organisms can recover; however, extreme cases can lead to complete shifts in benthic community.

Since the 1970s, the number of recognized coral diseases dramatically increased (Goreau et al. 1998; Richardson 1998; Humann and DeLoach 2002), and the reported number of epizootics resulting in significant scleractinian loss increased (Goreau et al. 1998; Raymundo et al. 2008). Two environmental drivers thought to increase disease prevalence, incidence, and progression are increased water temperature (Bruno et al. 2007; Muller et al. 2008) and decreased water quality due to increased nutrient and terrigenous sediments (Bruno et al. 2003; Voss and Richardson 2006). Increased temperatures may enhance diseases effects by either weakening host's immune systems or enhancing the causative agent's virulence (Raymundo et al. 2008). For example, outbreaks of coral diseases occurred following the 2005 Caribbean-wide bleaching event (Bruno et al. 2007; Muller et al. 2008) leading to extensive mortality in at least one location (Miller et al. 2006). Decreased water quality may reduce host disease resistance, increase disease virulence, and introduce pathogens into the benthic community (Bruno et al. 2003; Voss and Richardson 2006; Raymundo et al. 2008). Despite the evidence supporting the links between these environmental factors and coral diseases, significant gaps in understanding the causes and consequences of coral diseases exist and require further investigation in order to develop appropriate conservation measures (Raymundo et al. 2008).

Hurricanes, as a disturbance, occurred throughout the development of contemporary reefs affecting the physical structure and biodiversity within coral reef ecosystems (Connell 1978; Rogers 1993; Gardner et al. 2005). They are natural phenomena formed through the interactions of sea surface temperatures, wind shear, moisture availability, and atmospheric stability, and there is evidence that increased sea-surface temperature increases hurricane intensity (Santer et al. 2006). These storm events mechanically alter coral reefs by fragmenting and toppling colonies through intense wave-action and suspending and transporting sediments resulting in reduced fecundity in fragmented and smothered colonies (Woodley et al. 1981; Harmelin-Vivien and Laboute 1986; Rogers 1993). The extent of damage following a hurricane depends on benthic community diversity, depth, ecological history, characteristics of dominant species, and

coincidence of other disturbances (Rogers 1993; Knowlton and Jackson 2001; Bries et al. 2004). Change in live scleractinian cover following hurricanes can vary from significant change (Woodley et al. 1981; Harmelin-Vivien and Laboute 1986; Sommerfield et al 2008) to little (Edmunds 2002; Bries et al. 2004). Additionally, recovery from hurricanes events can vary from a few years to decades, even within reef tracts (e.g., Sommerfield et al 2008), depending on the severity of damage and the dominant scleractinian (Rogers 1993; Edmunds 2002); locations dominated by branching morphologies recover faster than locations dominated by massive morphologies (Rogers 1993; Knowlton and Jackson 2001). In at least one case, hurricanes and other disturbances facilitated a phase shift to an alternative state; Jamaican reefs collapsed and shifted to a macroalgae dominated state due to the combined effects of two hurricanes, the *Diadema antillarum* die-off in the early 1980s, and over-fishing (Hughes 1994; Gardner et al. 2005). Some researchers predict that increasing sea surface temperatures will lead to increased frequency and intensity of hurricanes; however, considerable uncertainty regarding this prediction exists (Santer et al. 2006). Even if intensity and frequency of hurricanes does not increase in the near future, they can facilitate phase shifts when coupled with other natural and anthropogenic disturbances (Hughes 1994; Gardner et al. 2005) and induce ecologically significant changes in reefs within MPA boundaries (Edmunds 2002).

Significant loss of scleractinian cover may induce a phase shift in the benthic community structure, such as coral dominated to algal dominated, resulting in an altered ecosystem (Hughes 1994; Done 1999). Benthic community members (e.g., scleractinians, gorgonians, poriferans, macroalgae) directly and indirectly compete for the limited resources (e.g., space, light, prey, and nutrients) within the coral reef ecosystem (Jackson 1977; Knowlton and Jackson 2001) and are subject to predation and disturbance. The net result of these ecological processes is a mosaic of organisms covering the hard substratum. An important process affecting the composition of this mosaic is herbivory (Knowlton and Jackson 2001). Grazing pressure by sea urchins and herbivorous fish contributes to the maintenance of scleractinian dominance by cropping macroalgae (Hay 1997; Paddock et al. 2006). However, fishing pressure (Hughes 1994; Mumby 2006) and disease outbreaks among herbivores, such as the Caribbean-wide epizootic in the echinoderm *Diadema antillarum* in 1982-1983 (Lessios et al. 1984), reduce herbivore

populations leading to reduced grazing pressure (Hughes 1994; Mumby 2006). Further, increased nutrient levels promote macroalgae growth (Littler et al. 1991) and disease progression (Voss and Richardson 2006). The combined loss of herbivores, elevated nutrients, and increased scleractinian morality can induce a phase shift from a mixed scleractinian/macroalgae state to a macroalgal-dominated state leading to a change in ecosystem function and a loss of associated goods and services (Hughes 1994; Done 1999).

Coral reef ecosystems provide many goods and services upon which humans have relied in the past, in the present, and into the future (Jackson 1997; Moberg and Folke 1999). Goods produced by coral reefs include seafood (Coblentz 1997; Jeffery and Jennings 1999; Warren-Rhodes et al. 2003), pharmaceuticals (Carté 1996; Hunt and Vincent 2006), aquaria ornamentals (Calado et al. 2003), building materials, and lime (Dulvy et al. 1995; Rajasuriya et al. 1995, Semesi et al. 1998). Moberg and Folke (1999) broadly categorized ecological services provided by coral reef ecosystems as physical services, biotic services, information services, and social services. Physical services include protecting shorelines by dissipating wave-energy thus reducing mechanical erosion of the shoreline (Mimura and Nunn 1998), contributing to atoll and carbonate island formation (Darwin 1962), and producing sediments (e.g., sand) found on beaches through mechanical erosion and bioerosion (Schlager 2005). Biotic services include supporting high biodiversity (Connell 1978; Jackson 1991; Gray 1997), fixing nitrogen (Wiebe et al. 1975; Capone and Carpenter, 1982), and acting as both CO_2 source and sink (Goreau 1990; Kayanne et al. 1995; Gattuso et al. 1996). Reef strata and scleractinian skeletal bands provide records of the environmental conditions during which they were deposited (Dodge and Gilbert 1984; Barnes and Lough 1996; Gagan et al. 1998), thus providing an information service to researchers (Moberg and Folke 1999). Humans directly rely on coral reef ecosystems for recreational opportunities (Hawkins and Roberts 1993), sustaining economic livelihood of coastal communities (Cesar et al. 1997), and supporting dietary needs (Johnstone et al. 1998). The continued decline of coral reef ecosystems will alter the availability of the goods produced and services rendered by these tropical ecosystems resulting in altered economic and ecological

processes (Wilkinson et al. 1996). Thus, it is necessary to reduce both natural and anthropogenic impacts when possible to further conservation of coral reef ecosystems.

Policy regarding coral reef conservation in the United States

Coral reef ecosystems within the U.S. Exclusive Economic Zone in the Pacific Ocean, tropical Atlantic Ocean, and the Caribbean Sea are estimated to cover approximately 179,872 km^2 (Rohmann et al. 2005). With past declines in ecosystem health and predicted increases in threats to and degradation within coral reef ecosystems in the near future, governments, non-government organizations (NGOs), and the research community have recognized the increasing need for coral reef conservation. Within the U.S. Federal government, the Executive and Legislative branches have issued policy documents with the purpose of promoting coral reef conservation (e.g., Clinton 1998; Bush 2006, 2007). NGOs have petitioned the government to increase conservation actions (CBD 2009), and the research community has called for increased conservation actions (Bellwood et al. 2004). Together, these groups' actions have shaped the current state of policy for the conservation of coral reefs within U.S. jurisdictions.

In 1998, President Clinton issued Executive Order 13089 (EO13089) to protect coral reef ecosystems within U.S. jurisdictions in an effort to further several congressional acts (Table 1, Clinton 1998). Under the Executive Order, federal agencies must 1) identify their actions that affect coral reef ecosystems, 2) protect and enhance coral reef ecosystems, and 3) ensure their future actions do not degrade coral reef ecosystems (Clinton 1998). EO13089 also created the United States Coral Reef Task Force (CRTF), which currently consists of 22 members, including 12 federal agencies, 7 U.S. states, territories, and commonwealths, and 3 freely associated states (CRTF 2009; Table 2). The responsibilities of the Task Force include a) mapping and monitoring, b) research, c) conservation, mitigation, and restoration, and d) international cooperation (Clinton 1998; CRTF 2001).

Table 8: Congressional Acts referenced by Executive Order 13089 (Clinton 1998) and the stated purpose of the acts.

Act (Year enacted)	Purpose (paraphrased from the Act)
Clean Water Act (1977)	1. Maintain the chemical, physical, and biological integrity of the Nation's waters; 2. When possible, provide for the protection and propagation of fish, shellfish, and wildlife; 3. Prohibit discharge of pollutants in toxic amounts; 4. Provide financial assistance to construct publicly owned waste-treatment works; 5. Develop and implement management plans assuring adequate control of pollutant sources; 6. Research and demonstrate technology to eliminate pollutant discharge; 7. Develop and implement programs to control non-point sources of pollution
Coastal Zone Management Act (1972)	1. Preserve, protect, develop, and enhance coastal zone resources; 2. Encourage and assist states in managing their coastal resources; 3. Encourage the use of special management areas; 4. Encourage participation of governmental partners and the public; 5. Encourage coordination between regulatory agencies
Magnuson-Stevens Fishery Conservation and Management Act (1976; amended 1996, 2006)	1. Take action to conserve and manage fisheries off the coasts of the United States; 2. Support implementation and enforcement of international fishery agreements for the conservation and management of migratory species; 3. Promote commercial and recreational fisheries; 4. Provide for the preparation and implementation of management to achieve and to maintain optimal yield; 5. Establish Regional Fishery Management Councils; 6. Encourage the development of currently under utilized fisheries; 7. Promote the protect of essential fish habitat
National Environmental Policy Act (1969)	1. Declare national policy to promote harmony between man and his environment; 2. Promote efforts to prevent or eliminate damage to the environment and biosphere; 3. Enrich understanding of ecological systems and natural resources; 4. Establish the Council on Environmental Quality
National Marine Sanctuaries Act (1972)	1. Identify and designate national marine sanctuary areas; 2. Provide authority for conservation and management of the sanctuaries; 3. Maintain biological communities with the sanctuaries; 4. Enhance public awareness of the resources managed by the National Marine Sanctuary System; 5. Support, promote, and coordinate research and long-term monitoring of these marine areas; 6. Facilitate non-prohibited public and private uses of these areas; 7. Develop and coordinate protection and management plans; 8. Create models of ways to conserve and manage resources; 9. Cooperate with global programs encouraging marine resource conservation
National Park Service Organic Act (1916)	1. Established the National Parks Service to promote and regulate use of national parks, monuments, and reservations with the purpose of conserving the natural resources within these areas and provide the enjoyment of these resources for future generations
National Wildlife Refuge System Administration Act (1966)	1. Provide for the conservation, protection and management of native wildlife species threatened with extinction; 2. Consolidate authorities relevant to the management of the National Wildlife Refuge System;

Table 9: Members of the U.S. Coral Reef Task Force and their role in the organization as identified in the U.S. Coral Reef Task Force Federal Member Coral Profiles (CRTF 2009b). Co-Chairs, Federal Agency Members, and State and Territory members are voting members. Freely Associated States members are non-voting members.

Member	Role
Department of Commerce	Co-Chair, Federal Agency Member
Department of Interior • National Oceanic and Atmospheric Administration • Fish and Wildlife Service • Minerals Management Service • The National Parks Service • Office of Insular Affairs • U.S. Geologic Service	Co-Chair, Federal Agency Member
U.S. Agency for International Development	Federal Agency Member
U.S. Department of Agriculture	Federal Agency Member
Department of Defense	Federal Agency Member
U.S. Department of Homeland Security, Coast Guard	Federal Agency Member
Department of Justice	Federal Agency Member
Department of State	Federal Agency Member
Department of Transportation	Federal Agency Member
Environmental Protection Agency	Federal Agency Member
National Aeronautic and Space Administration	Federal Agency Member
National Science Foundation	Federal Agency Member
Commonwealth of Northern Mariana Islands	State and Territory Member
Commonwealth of Puerto Rico	State and Territory Member
State of Florida	State and Territory Member
State of Hawaii	State and Territory Member
Territory of Guam	State and Territory Member
Territory of American Samoa	State and Territory Member
Territory of the U.S. Virgin Islands	State and Territory Member
Federated States of Micronesia	Freely Associated State
Republic of Marshall Islands	Freely Associated State
Republic of Palau	Freely Associated State

In 2000, the CRTF adopted the "National Action Plan to Conserve Coral Reefs" ("Action Plan") as a comprehensive roadmap to long-term conservation of coral reefs within U.S. jurisdictions (CRTF 2000). In 2002, the CRTF created a complementary document entitled, "A National Coral Reef Action Strategy" ("Action Strategy")

outlining 13 strategies for short-term conservation of coral reef ecosystems (CRTF 2009a). The Action Plan identified pollution, overfishing, overuse, destructive fishing practices, dredging, shoreline modification, vessel groundings and anchoring, disease outbreaks, and global climate change as major threats to coral reef ecosystems (CRTF 2000). The document also identified and described core principles necessary to conserving coral reef ecosystems (Table 3). Beyond these principals, the Action Plan separated necessary conservation actions into the themes of "Understanding Coral Reef Ecosystems" and "Reduce the Adverse Impacts of Human Activities," (CRTF 2000). In order to understand coral reef ecosystems, the Action Plan identified three necessary actions: 1) comprehensive mapping, assessment, and monitoring, 2) strategic research on regional threats and underlying ecological processes, and 3) incorporating the human dimension into conservation and management (CRTF 2000). Further, the Action Plan identified a) creating a network of Marine Protected Areas (MPAs), b) reducing adverse effects of extractive uses, c) reducing habitat destruction, pollution, and international trade, d) restoring damaged reefs, e) strengthening international activities, f) improving governmental accountability, and g) informing and engaging the public as essential actions to reducing human impacts on coral reef ecosystems (CRTF 2000). The combination of core principals and actions detailed within the Action Plan provided a comprehensive strategy and guiding document for conserving coral reef ecosystems within U.S. jurisdictions.

Table 10: Core principals identified by the Action Plan.

Principle
▪ Adopt a science-based ecosystem approach to conservation ▪ Employ adaptive management to track and respond to change and emerging threats ▪ Take appropriate, precautionary measures ▪ Incorporate the human dimensions into conservation actions ▪ Apply marine zoning, such as marine protected areas and no-take reserves, to minimize harmful human actions ▪ Use existing management authorities and programs and develop new legal mechanisms for conservation ▪ Develop and supporting domestic partnerships to meet cross-jurisdictional challenges ▪ Provide leadership to reduce global threats

In June 2000, the CRTF presented the Action Plan to the U.S. Congress, and, in December of the same year, the U.S. Congress enacted the Coral Reef Conservation Act of 2000 (CRCA 2000), which provided congressional funding for coral reef conservation efforts through Coral Reef Conservation Program (CRCP) within the National Oceanic and Atmospheric Administration (NOAA). The stated purpose of the CRCA was to preserve coral reef ecosystems, to promote wise management and sustainable use, to develop scientific information on the condition and threats to coral reefs, to support conservation programs to assist in preservation, to support those conservation programs financially, and to establish mechanisms for collecting and allocating donations from the private sector (CRCA 2000). To achieve these goals, the CRCA required an implementation plan which addressed coastal uses and management; water and air quality; mapping and information management; research, monitoring, and assessment; international and regional issues; outreach and education; local strategies; and conservation including MPAs (CRCA 2000). As required by the CRCA (2000), the CRTF developed and adopted the Action Strategy (CRTF 2009a). Together, the CRCA (2000), Action Plan, and Action Strategy are complementary documents providing financial and policy support necessary to conserve coral reef ecosystems within U.S. jurisdictions, yet they are not the only policy avenues available for coral reef conservation.

In 2006, NOAA's National Marine Fisheries Service (NMFS) listed two scleractinian species, Staghorn coral and Elkhorn coral (*Acropora cervicornis* and *Acropora palmata*, respectively), as threatened under the Endangered Species Act of 1973 (ESA 1973), and designated critical habitat for the two species, which includes areas in Florida, Puerto Rico, and the U.S. Virgin Islands (NOAA 2006, 2008). The ESA provides a policy framework for implementing conservation actions to maintain and to restore imperiled species' populations (ESA 1973). The two scleractinians were the second and third marine invertebrates listed under the ESA with White abalone (*Haliotis sorenseni*) being the first marine invertebrate to be listed (NOAA 2001). In February 2010, the NMFS initiated an ESA Status Review listing 82 scleractinians (7 Caribbean species and 75 Pacific species) as candidate species (NOAA 2010) following a petition

by the Center for Biological Diversity (CBD 2009). The Caribbean species include *Agaricia lamarcki*, *Dendrogyra cylindrus*, *Dichocoenia stokesii*, *Montastraea annularis*, *M. faveolata*, *M. franskii*, and *Mycetophyllia ferox* (NOAA 2010); all seven species inhabit the patch reefs of La Parguera, Puerto Rico (Ballantine et al. 2008). While the ESA provides a policy avenue for protecting individual species and their critical habitat, the National Marine Sanctuaries Act (NMSA 1972) provides a policy avenue to protect and to conserve coral ecosystems and their resources.

NOAA's Office of National Marine Sanctuaries (ONMS) manages coral reef ecosystems within three sanctuaries and one national monument. The NMSA (1972) established the ONMS to administer the marine sanctuaries network and meet the goals of the NMSA (1972). Four areas managed by the ONMS contain coral reefs; three are National Marine Sanctuaries and one is a Marine National Monument. President George W. Bush established the Northwestern Hawaiian Islands Marine National Monument by Presidential Proclamation 8031 (Bush 2006). The Monument's name was later amended to the Papahanaumokuakea Marine National Monument (Bush 2009). Located in the Pacific Ocean, the Monument protects approximately 140,000 mi^2. Also located in the Hawaiian Archipelago, the Hawaiian Islands Humpback Whale National Marine Sanctuary covers approximately 1400 mi^2 and was established to protect the calving grounds of Humpback whales (*Megaptera novaeangliae*) (HIHWNMS 2002); coral reefs incidentally occur within its boundaries (Aki et al 1994; HIHWNMS 2002). The Fagatele Bay National Marine Sanctuary in American Samoa is the smallest region administered by the ONMS encompassing approximately 0.25 m^2. The Florida Keys National Marine Sanctuary encompasses areas in the western Atlantic Ocean and the eastern Gulf of Mexico covering approximately 2800 mi^2.

The need for increased conservation efforts in coral reef ecosystems was recognized at the 11^{th} International Coral Reef Symposium (ICRS) in 2008. The 11^{th} ICRS resulted in a Call-to-Action (ICRS Local Organizing Committee 2008), which identified three primary steps needed to protect coral reef ecosystems: 1) improve existing and increase planned local action to develop stewardship of coral reef resources, 2) implement marine protected areas (MPAs), and 3) develop and implement restoration techniques (ICRS Local Organizing Committee 2008). Further, the Call-to-Action

identifies the need to incorporate stakeholder communities, engage government at multiple levels (e.g., local, state, and federal), establish legislative and regulatory authorities, and conduct needed science as essential to protecting coral reefs (ICRS Local Organizing Committee 2008).

Marine protected areas (MPAs) are becoming more common as tools for the protection and management of marine ecosystems because they can be designed to meet many different goals (NRC 2001; Palumbi 2001). The National Research Council (2001) defined MPAs as, "areas designated for special protection to enhance the management of marine resources" (NRC 2001). Palumbi (2001) described three broad categories for MPA designation: fisheries focused, ecosystem diversity focused, and special-area focused. Fisheries focused MPAs are designed to enhance the fisheries yields over larger areas by restricting or regulating extractive use within a designated area, and biodiversity reserves are designed to preserve biodiversity by reducing and regulating activities within an area (Palumbi 2001). Special-area focused MPAs are designated to protect geographic features with cultural or biological significance (Palumbi 2001). Palumbi (2001) identified another important characteristic of MPAs as the spatial extent of their effects: local or regional (Palumbi 2001). A local effect means that the MPA benefits the enclosed area, and a regional effect means that the MPA benefits the area outside its boundaries (Palumbi 2001).

As a conservation tool, MPAs show promise as components of integrated management schemes (NRC 2001; Palumbi 2001); however, controversy often surrounds MPA implementation (NRC 2001; Palumbi 2001). The controversy often stems from political resistance to closing areas which have been traditionally open to use for all users (NRC 2001) and scientific uncertainty regarding optimal MPA design and placement, ecological processes (e.g., larval dispersal, site fidelity) affecting and affected by MPAs, and the evaluation of the economic costs and benefits associated with MPAs (NRC 2001; Palumbi 2001). Further, evaluating MPA efficacy is difficult and requires two levels of analysis: 1) a local comparison identifying if MPAs meet their individual goals and 2) a broader comparison identify if MPAs have local or regional effects, in general (Palumbi 2001). Each MPA is a unique area due to its topographic, ecological, and social conditions resulting in unreplicated sampling locations, and ecological studies in the field

do not have the controls of ecological studies in the lab meaning that caution must be taken when interpreting the results of field studies. Despite the controversy and scientific uncertainty, MPAs are often promoted as important tools for coral reef conservation (NRC 2001; Palumbi 2001; CRTF 2000; CRCA 2002; ICRS Local Organizing Committee 2008), and recent research suggests that MPAs benefit coral reef ecosystems.

Selig and Bruno (2010) compared long-term changes in coral cover (1969-2006) using a global database containing 5170 independent surveys on 310 reefs within MPAs and 3364 surveys on unprotected reefs. They reported no change in coral cover within reefs protected by MPAs and declines in coral cover on unprotected reefs (Selig and Bruno 2010). Selig and Bruno (2010) also found that effectiveness in preventing coral cover depended on length of protection for the MPA with coral cover on Caribbean reefs declining for 14 years, with less decline each year, following MPA implementation before beginning to increase (Selig and Bruno 2010). In the Indo-Pacific, coral cover continued to decline for 4 years following MPA implementation before beginning to increase (Selig and Bruno 2010).

Remote Sensing of Coral Reefs

Remote observation has been identified as an important tool in the conservation of coral reef ecosystems by both policy makers and researchers. Mapping of coral reef ecosystems was explicitly identified as an important conservation action in Executive Order 130789 (Clinton 1998), the National Action Plan for Coral Reef Conservation (CRTF 2000), and the Coral Reef Conservation Act (CRCA 2000). The Call-to-Action by the International Coral Reef Symposium's Local Organizing Committee emphasized the use of mapping to improve visualization of changes within the coral reef ecosystems and provide improved products for decisions regarding coral reef resources (ICRS Local Organizing Committee 2008). On a broader scale, the Interagency Ocean Policy Task Force (IOPTF) identified remote observation of marine systems using unmanned vehicles and satellite platforms as a necessary tool "in meeting the Nation's stewardship responsibilities" (IOPTF 2010).

Using remotely sensed data to inform research and policy is not new to the marine sciences. Acoustics (e.g., sonar and telemetry) have been used to map bathymetry

(Mobley et al. 2005; Purkis 2005), identify fish species and size distributions (McClatchie et al. 2000), track fish movement (Starr et al. 2004), and estimate fish site fidelity (Lindholm et al. 2007). Satellite and sub-orbital platforms with spectral-based instruments have been used to map bathymetry (Brock et al. 2004; Reigl et al. 2009) and observe sea ice concentration (Drüe and Heinemann 2005; Laine 2008), sea surface temperature (Liu et al. 2004), and ocean color (Carder et al. 1999, Acker et al. 2004). Products derived from these data inform managers on resource distributions, potential threats, and change in resources over time. For example, the National Oceanic and Atmospheric Administration (NOAA) produces the Coral Bleaching Alerts based on remotely-sensed sea surface temperature data to indicate the potential for bleaching within regions (NOAA 2009), and acoustics are used to identify fish species and size-distributions for the management of commercially important fisheries in New Zealand (McClatchie et al. 2000).

In recent years, remotely sensed data of tropical marine ecosystems from multispectral and hyperspectral sensors on space-borne (i.e., satellite) or suborbital platforms (i.e., airplanes and unmanned aircraft systems) have become more common (Peterson et al. 2003; Andréfouët and Reigl 2004) for these purposes. Despite this success, technical and logistical limitations constrain the accurate identification of reef community structure by both hyperspectral and multispectral sensor systems (Lubin et al. 2001; Andréfouët et al. 2002; Joyce et al. 2004). Coral reef benthic types show reflectance peaks between 550 and 650 nm requiring imaging spectrometers and multispectral imaging systems to be optimized in the visible range (400 nm to 650 nm) and have a high signal-to-noise ratio over dark targets (e.g., water) to gather spectral information from benthic targets in shallow reef ecosystems (Guild et al. 2009; Lobitz et al. 2009). Further, integrating *in situ* spectra for classification training and pixel linear unmixing improves classification accuracy (Hochberg et al. 2003; Hedley and Mumby 2003; Purkis and Pasterkamp 2003; Mobley et al. 2005; Purkis 2005; Guild et al. 2009). However, gaps in matching *in situ* spectra with remote sensing data exist due to light attenuation and scattering in the atmosphere and water columns (Hochberg et al. 2003; Hochberg et al. 2004; Lobitz et al. 2009), sun glint effects at the air-water interface, and the difference in the spatial scale of these measurements.

Remote sensing data have been used to observe mesoscale patterns in sea-surface temperatures and to identify the potential for bleaching at the region-wide scale (Donner et al. 2007; Wilkinson and Souter 2008). In 2005, a massive bleaching event occurred throughout the Caribbean due to elevated sea-surface temperatures, which persisted for months, resulting in mass mortality and disease outbreaks (Miller et al. 2006; Donner et al. 2007; Whelan et al. 2007; Oxenford et al. 2008; Muller et al. 2008; Rowlands et al. 2008; Steiner and Kerr 2008; Wilkinson and Souter 2008). During the bleaching event, NOAA used AVHRR imagery to monitor the development of sea surface temperature anomalies (i.e., hotspots) producing images for "HotSpots" (Figure 18) and "Degree Heating Weeks" (DHW; Figure 19). The information was used to produce "Bleaching Watch Alerts" (BWA) to warn researchers and managers of the potential for bleaching (Wilkinson and Souter 2008). The BWA alerted the coral reef community of a large-scale disturbance allowing researchers and managers to prepare monitoring efforts to quantify the extent and duration of the bleaching event, and they provided a historical record of the sea-surface temperatures allowing for comparisons with future events when they occur (Wilkinson and Souter 2008).

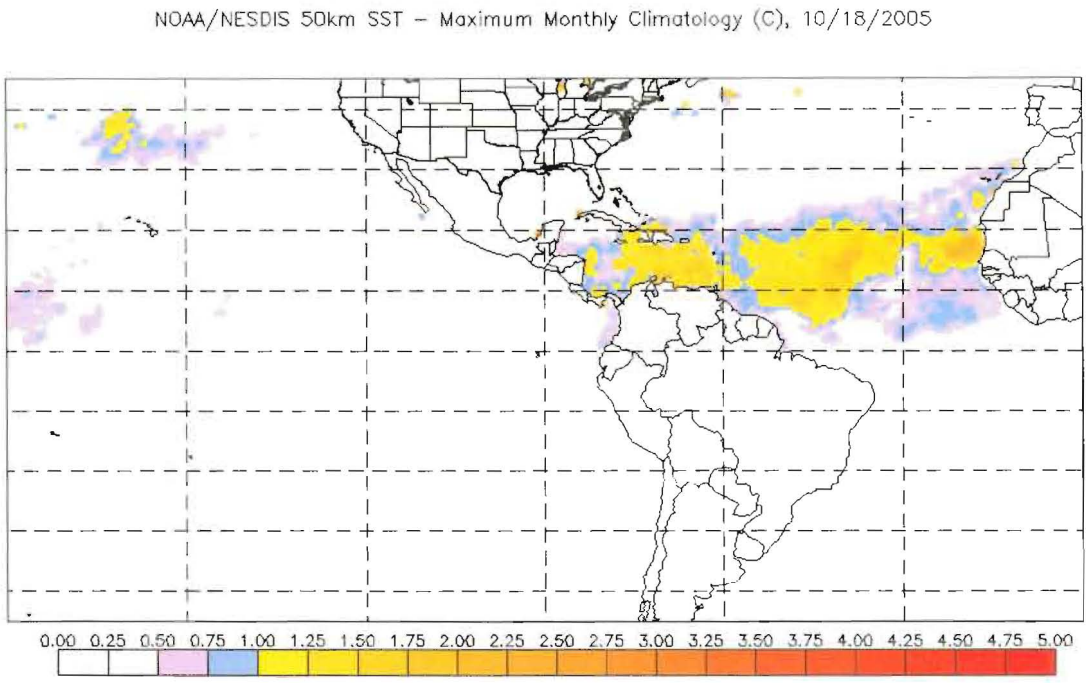

Figure 18: HotSpots image produced by NOAA's coral watch program showing the thermal anomaly that induced bleaching in the western Atlantic Ocean (Image source: NOAA Coral Reef Watch, http://www.osdpd.noaa.gov/data/cb/hotspots/2005/hotspotw.10.18.2005.gif).

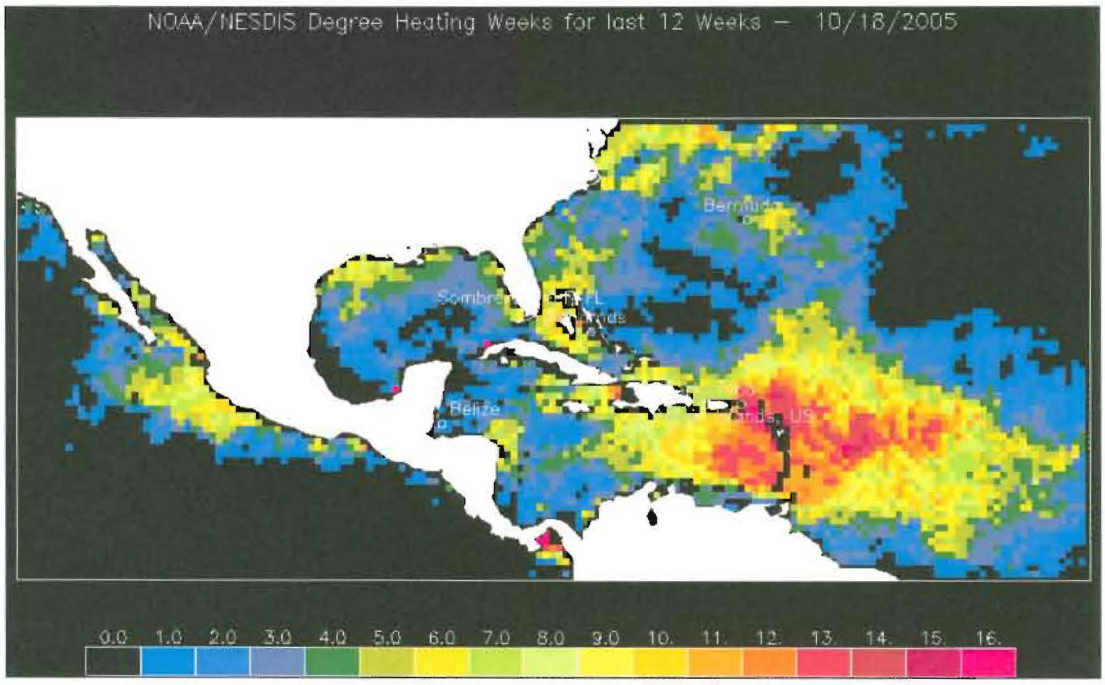

Figure 19: Degree heating weeks (DHW) image produced by NOAA's coral watch program showing the thermal anomaly that induced bleaching in the western Atlantic Ocean (Image source: NOAA Coral Reef Watch, http://www.osdpd.noaa.gov/data/cb/dhw/2005/dhwa.10.18.2005.gif).

Summary

Coral reef ecosystems provide valuable ecosystem goods and services; however, their health and resilience has declined due to natural and anthropogenic factors. Furthermore, these declines are predicted to continue in the near future. Due to these declines, the need for coral reef conservation has been recognized within the research community, the federal government, and among non-government organizations leading to an increase in conservation actions. Specific avenues promoted for coral reef conservation is the implementation of MPAs and the mapping of shallow coral reefs using remotely-sensed data. MPAs have been shown to benefit marine ecosystems; however, controversy surrounds their implementation. Maps derived from remotely-sensed data allow visualization of the spatial distribution of marine resources and; however, technical and logistical limitations constrain the information derived for shallow water ecosystems. The development and improvement of techniques for map production and the application of landscape ecology principles and derivation of ecological information needed by resource managers from these products are active areas of research, and progress made in these areas will benefit both scientific understanding and conservation of coral reef ecosystems.

References

Acker JG, Vasilkov A, Nadeau D, Kuring N. 2004. Use of SeaWiFS ocean color data to estimate neritic sediment mass transport from carbonate platforms for two hurricane-forced events. Coral Reefs. 23(1):39-47.

Aki K, Brock R, Miller J, Mobley JR, Rappa PJ, Tarnas D, Yuen M. [1994] A site characterization study for the Hawaiian Islands Humpback Whale National Marine Sanctuary. [Internet] [cited: 2010 May 10]. Available from: http://hawaiihumpbackwhale.noaa.gov/documents/pdfs_management/sitecharacterization.pdf

Andrefouet S, Berkelmans R, Odriozola L, Done T, Oliver J, Muller-Karger F. 2002. Choosing the appropriate spatial resolution for monitoring coral bleaching events using remote sensing. Coral Reefs 21(2):147-154.

Andrefouet S and Reigl B. 2004. Remote sensing: a key tool for interdisciplinary assessment of coral reefs processes. Coral Reefs 23(1):1-4.

Ballantine DL, Appledoorn RS, Yoshioka P, Weil E, Armstrong R, Garcia JR, Otero E, Pagan F, Sherman C, Hernandez-Delgado EA, Bruckner A, Lilyestrom C. 2008. Biology

and ecology of Puerto Rican coral reefs. In: Coral reefs of the USA. BM Riegl and RE Dodge (Eds). Berlin: Springer Science and Business Media.

Barnes DJ and Lough JM. 1996. Coral skeletons: storage and recovery of environmental information. Global Conservation Biology. 2(6):569-582.

Barton AD and Casey KS. 2005. Climatological context for large-scale coral bleaching. Coral Reefs 24(4):536-554.

Bellwood DR, Hughes TP, Folke C, Nyström M. 2004. Confronting the coral reef crisis. Nature. 429:827-833.

Berkelmans R and Oliver J. 1999. Large-scale bleaching of corals on the Great Barrier Reef. Coral Reefs 18(1):55-60.

Bries JM, Debrot AO, Meyer DL. 2004. Damage to the leeward reefs of Curacao and Bonaire, Netherlands Antilles from a rare storm event: Hurricane Lenny, November 1999. Coral Reefs 23(2):297-307.

Brock J, Wright C, Clayton T, Nayegandhi A. 2004. Lidar optical rugosity of coral reefs in Biscayne National Park, Florida. Coral Reefs. 23(1):48-59.

Brown BE, Dunne RP, Goodson MS, and Douglas AE. 2002. Experience shapes the susceptibility of a reef coral to bleaching. Coral Reefs 21(2):119-126.

Bruno JF, Petes LF, Harvell CD, Hettinger A. 2003. Nutrient enrichment can increase the severity of coral diseases. Ecology Letters. 6(12):1056-1061.

Bruno JF, Selig ER, Casey KS, Page CA, Willis BL, Harvell CD, Sweatman H, Melendy AM. 2007. Thermal stress and coral cover as drivers of coral disease outbreaks. Public Library of Science Biology 5(8):1-8.

Bush GW. 2006. Presidential Proclamation 8031 of June 15, 2006: Establishment of the Northwestern Hawaiian Islands Marine National Monument. Federal Regitrar. 71(122):36443-36475.

Bush GW. 2007. Presidential Proclamation 8112 of February, 2007: Amending Proclamation 8031 of June 15, 2006 to read "Establishment of the Papahanaumokuakea Marine National Monument." Federal Regitrar. 72(143):10031.

Bythell JC, Gladfelter EH, Bythell M. 1993. Chronic and catastrophic natural mortality of three common Caribbean corals. Coral Reefs 12(3-4):143-152.

Calado R, Lin J, Rhyne AL, Araújo R, Narciso L. 2003. Marine ornamental decapods: popular, pricey, and poorly studied. Journal of Crustacean Biology. 23(4):963-973.

Capone DG and Carpenter EJ. 1982. Nitrogen fixation in the marine environment. Science. 217(4565):1140-1142.

Carder KL, Chen FR, Lee ZP, Hawes S, Kamykowski D. 1999. Semi-analytic MODIS algorithms for chlorophyll a and absorption with bio-optical domains based on nitrate depletion temperatures. J Geophys Res 103(C3):5403-5421

[CBD] Center for Biological Diversity. 2009. Petition to list 83 coral species under the Endangered Species Act. [Internet]. [cited 25 February 2010]. Available from: http://sero.nmfs.noaa.gov/pr/esa/pdf/091020_CBD_Coral_Petition.pdf

Cesar H, Lundin CG, Betterncourt S, Dixon J. 1997. Indonesian coral reefs: an economic analysis of a precious but threatened resource. Ambio. 26(6):345-350.

Clinton WJ. 1998. Executive Order 13089: Coral Reef Protection. Office of the Press Secretary.

Coblentz BE. 1997. Consumption of coral reef fish suggests non-sustainable extraction. Conservation Biology. 11(2):559-561.

Connell JH. 1978. Diversity in tropical rain forests and coral reefs. Science 199(4335):1302-1310.

Cook CB, Logan A, Ward J, Lockhurst B, Berg Jr CJ. 1990. Elevated temperatures and bleaching on a high latitude coral reef: the 1988 Bermuda event. Coral Reefs 9(1):45-49.

Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill R, Paruelo J, Raskin R, Sutton P, van den Belt M. 1997. The value of the world's ecosystem services and natural capital. Nature. 387:253-260

[CRAN] Comprehensive R Archive Network. [date unknown]. The Comprehensive R Archive Network. [Internet]. [cited 2009 December 21]. Available from: http://cran.r-project.org/

Croyle Z. 2009. Analysis of baseflow trends related to upland groundwater pumping for Las Garzas, San Clemente, Potrero, and San Jose creeks. [MSc thesis]. Seaside (CA): California State University Monterey Bay. 116 p. Available from: http://sep.csumb.edu/cwsp/theses/Croyle_Thesis_090422.pdf

[CRTF] U.S. Coral Reef Task Force. [2000]. National Action Plan to Conserve Coral Reefs. [Internet]. [cited: 2010 May 4] Available from: http://coralreef.gov/about/CRTFAxnPlan9.pdf

[CRTF] U.S. Coral Reef Task Force. [2001]. U.S. Coral Reef Task Force Charter. [Internet]. [cited: 2010 May 4] Available from: http://coralreef.gov/about/charter document.pdf

[CRTF] U.S. Coral Reef Task Force. [2009a]. U.S. Coral Reef Task Force Documents and Policies. [Internet]. [cited: 2010 May 4] Available from: http://coralreef.gov/about/docs.html

[CRTF] U.S. Coral Reef Task Force. 2009b. U.S. Coral Reef Task Force Federal Member Profiles. [Internet]. [cited: 2010 May 4] Available from: http://coralreef.gov/about/coralpupdated.pdf

D'Croz L and J L Mate. 2004. Experimental responses to elevated water temperatures in genotypes of the reef coral Pocillopora damicornis from upwelling and non-upwelling environments in Panama. Coral Reefs 23(4):473-483.

Darwin, C. 1962. The structure and distribution of coral reefs. (1st Edition: Reprint). Berkeley and Los Angeles: University of California Press.

Dodge RE and Gilbert TR. 1984. Chronology of lead pollution contained in banded coral skeletons. Marine Biology. 82(1):9-13.

Done TJ. 1999. Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. American Zoologist 39:66-79.

Done TJ and Jones R. 2006. Tropical coastal ecosystems and climate change prediction: global and local risks. In: Coral reefs and climate change: science and management, pp. 5-32. Coastal and Estuarine Studies (61). American Geophysical Union.

Donner SD, Skirving WJ, Little CM, Oppenheimer M, Hoegh-Guldberg O. 2005. Global assessment of coral bleaching and required rates of adaptation under climate change. Global Change Biology 11:2251-2265.

Donner SD, Knutson TR, Oppenheimer. 2007. Model-based assessment of the role of human-induced climate change in the 2005 Caribbean coral bleaching event. Proceedings of the National Academy of Science. 104(13):5483-5488.

Drüe C and Heinemann G. 2005. Accuracy assessment of sea-ice concentrations from MODIS using in-situ measurements. Remote Sensing of Environment. 95:139-149

Dulvy NK, Stanwell-Smith D, Darwall WRT, Horrill CJ. 1995. Coral mining at Mafia Island, Tanzania: a management dilemma. Ambio. 24(6):358-365

Edmunds PJ. 2002. Long-term dynamics of coral reefs in St. John, US Virgin Islands. Coral Reefs/ 21(4):357-367.

Faure G. 1989. Degradation of coral reefs at Moorea Island (French Polynesia) by *Acanthaster planci*. Journal of Coastal Research. 5(2):295-305.

Fenner D and Banks K. 2004. Orange cup coral Tubastraea coccinea invades Florida and the Flower Garden Banks, Northwestern Gulf of Mexico. Coral Reefs 23(4):505-507.

Finelli CM, Helmuth BST, Pentcheff ND, Wethy DS. 2006. Water flow influences oxygen transport and photosynthetic efficiency in corals. Coral Reefs 25(1):47-57.

Fitt WK, Brown BE, Warner ME, Dunne RP. 2001. Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. Coral Reefs 20(1):51-65.

Fox HE and Caldwell RL. 2006. Recovery from blast fishing on coral reefs: a tale of two scales. Ecological Applications. 16(5):1631-1635

Gagan MK, Ayliffe LK, Hopley D, Cali JA, Mortimer GE, Chappell J, McCulloh MT, Head MJ. 1998. Temperatue and surface-ocean water balance of the mid0Holocene Tropical Western Pacific. Science. 279(5353):1014-1018.

Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR. 2003. Long-term region-wide decline in Caribbean corals. Science 301(5635):958-960.

Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR. 2005. Hurricanes and Caribbean coral reefs: impacts, recovery patterns, and role in long-term decline. Ecology 86(1):174-184.

Gates RD. 1990. Seawater temperature and sublethal bleaching in Jamaica. Coral Reefs, 8(4): 193-197.

Gattuso JP, Frankignoulle M, Smith SV, Ware JR, wollast R, Buddemeier RW, Kayanne H. 1996. Coral reefs and carbon dioxide. Science. 271(5253):1298-1300.

Gleason MG. 1993. Effects of disturbance on coral communities: bleaching in Moorea, French Polynesia. Coral Reefs 12(3-4):193-201.

Glynn PW. 1993. Coral reef bleaching: ecological perspectives. Coral Reefs 12(1):1-17.

Golbuu Y, Victor S, Penland L, Idip D, Emaurois C, Okaji K, Yukihira H, Iwase A, van Woesik R. 2007. Palau's coral reefs show differential habitat recovery following the 1998-bleaching event. Coral Reefs 26(2):319-332.

Goreau TF. 1964. Mass expulsion of zooxanthellae from Jamaican reef communities after Hurricane Flora. Science 145:383-386.

Goreau TJ. 1990. Balancing atmospheric carbon dioxide. Ambio. 19(5):230-236.

Goreau TJ and Macfarlane AH. 1990. Reduced growth rate of Montastraea annularis following the 1987-1988 coral-bleaching event. Coral Reefs 8(4):211-215.

Goreau TJ, Cervino J, Goreau M, Hayes R, Hayes M, Richardson L, Smith G, DeMeyer K, Nagelkerken I, Garzon-Ferrera J, Gil D, Garrison G, Williams EH, Bunkley-Williams L, Quirolo C, Patterson K, Porter JW, Porter K. 1998. Rapid spread of diseases in Caribbean coral reefs. Revista Biological Tropical. 46(Supl. 5):157-171.

Gray JS. 1997. Marine biodiversity: patterns, threats and conservation needs. Biodiversity and Conservation. 6(1):153-175.

Guild L, Lobitz B, Armstrong R, Gilbes F, Goodman J, Detres Y, Berthold R, Kerr J. 2009. NASA airborne AVIRIS and DCS remote sensing of coral reefs. Paper, Proceedings 11th International Coral Reef Symposium. Ft. Lauderdale, FL, July 2008.

Harmelin-Vivien ML and Laboute P. 1986. Catastrophic impacts of hurricanes on atoll outer reef slopes in the Taumotu (French Polynesia). Coral Reefs. 5(1):55-62.

[HIHWNMS] Hawaiian Islands Humpback Whale National Marine Sanctuary. 2002. Hawaiian Islands Humpback Whale National Marine Sanctuary Management Plan. [Internet] [cited: 10 May 2010] Available from: http://hawaiianhumpbackwhale.noaa.gov/documents/pdfs_mpr/HIHWNMS_FMP.pdf

Hawkins JP and Roberts CM. 1993. Effects of recreational scuba diving on coral reefs: trampling on reef-flat communities. Journal of Applied Ecology. 30(1):25-30.

Hay ME. 1997. The ecology and evolution of seaweed-herbivore interactions on coral reefs. Coral Reefs. 16(Suppl 1):S67-S76.

Hayes RL and Bush PG. 1990. Microscopic observations of recovery in the reef-building scleractinian coral, Montastraea annularis, after bleaching on a Cayman reef. Coral Reefs 8(4):203-209.

Hedley JD and Mumby PJ. 2003. A remote sensing method for resolving depth and subpixel composition of aquatic benthos. Limnology and Oceanography 48:480-488.

Hochberg EJ, Andrefouet S, Tyler MR. 2003. Sea surface correction of high spatial resolution Ikonos images to improve bottom mapping in near-shore environments. IEEE Transactions on Geoscience and Remote Sensing 41(7):1724-1729.

Hochberg EJ, Atkinson MJ, April A, Andrefouet S. 2004. Spectral reflectance of coral. Coral Reefs 23(1):84-95.

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Muthiga NA, Bradbury RH, Dubi A, Hatziolos ME. 2007. Coral reefs under rapid climate change and ocean acidification. Science 318:1737-1742.

Hughes TP. 1994. Catastrophes, phase shifts, and large-scale degredation of a Caribbean coral reef. Science. 265(5178):1547-1551

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas JA, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301(5635):929-933.

Humann P and DeLoach N. 2002. Reef Coral Identification. Second. Jacksonville: New World Publications, Inc.

Hunt B and Vincent ACJ. 2006. Scale and sustainability of marine bioprospecting for pharmaceuticals. Ambio. 35(2):57-64.

ICRS Local Organizing Committee. 2008. Official outcomes and call to action of the 11th International Coral Reef Symposium. [Internet] [cited 2009 December 14] Available from: http://www.nova.edu/ncri/11icrs/11icrs_outcomes_calltoaction.pdf.

[IOPTF] Interagency Ocean Policy Task Force. 2010. Final recommendations of the Interagency Policy Task Force. . [Internet]. [cited 2010 December 20]. Available from: http://www.whitehouse.gov/files/documents/OPTF_FinalRecs.pdf

Jackson JBC. 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. American Naturalist. 111(980):734-767.

Jackson JBC. 1991. Adaptation and diversity in reef corals. BioScience. 41(7):475-482.

Jackson JBC. 1997. Reefs since Columbus. Coral Reefs 16:S23-S32.

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science. 293(5530):629-638.

Jeffery FG and Jennings CA. 1999. An alternative view on estimating subsistence consumption of coral reef fishes in the U.S. Virgin Islands. Conservation Biology. 13(4):939-941.

Johnstone RW, Muhando CA, Francis J. 1998. The status of the coral reefs of Zanzibar: one example of a regional predicament. Ambio. 27(8):700-707.

Joyce KE, Phinn SR, Roelfsema CM, Neil DT, Dennison WC. 2004. Combining Landsat ETM+ and Reef Check classifications for mapping coral reefs: a critical assessment from the Great Barrier Reef, Australia. Coral Reefs 23(1): 21-25.

Kleypas JA, Buddemeier RW, Archer D, Gattuso JP, Langdon C, Opdyke BN. 1999. Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. Science 284(5411): 118-120.

Kleypas JA and Langdon C. 2006. Coral reefs and changing seawater carbonate chemistry. In Coral reefs and climate change: science and management, 73-110. Coastal and Estuarine Studies (61), American Geophysical Union.

Knowlton NC and Jackson JBC. 2001. The ecology of coral reefs. In: Marine Community Ecology. Bertness MW, Gaines SD, Hay ME (Eds.). Sunderland, Massachusetts. Sinauer Associates, Inc.

Laine V. 2008. Antarctic ice sheet and sea ice regional albedo and temperature change, 1981-2000, from AVHRR Polar Pathfinder data. Remote Sensing of Environment. 112:646-667

Lasker HR, Peters EC, Coffroth MA. 1984. Bleaching of reef coelenterates in the San Blas Islands, Panama. Coral Reefs 3(4):183-190.

Leder JJ, Szmant AM, Swart PK. 1991. The effect of prolonged "bleaching" on skeletal banding and stable isotopic composition in Montastraea annularis. Coral Reefs 10(1): 19-27.

Lesser MP, Stochaj WR, Tapley DW, Shick JM. 1990. Bleaching in coral reef anthozoans: effects of irradiance, ultraviolet radiation, and temperature on the activities of protective enzymes against active oxygen. Coral Reefs 8(4):225-232.

Lesser MP. 1997. Oxidative stress causes coral bleaching during exposure to elevated temperatures. Coral Reefs 16(3):187-192.

Lesser MP and Farrell JH. 2004. Exposure to solar radiation increases damage to both host tissues and algal symbionts of corals during thermal stress. Coral Reefs 23(3): 367-377.

Lessios HA, Robertson DR, Cubit JD. 1984. Spread of *Diadema* mass mortality through the Caribbean. Science. 226(4672):335-337.

Lindholm J, Auster PJ, Knight A. 2007. Site fidelity and movement of adult Atlantic cod Gadus morhua at deep boulder reefs in the western Gulf of Maine, USA. Marine Ecology Progress Series 342:239-247

Littler MM, Littler DS, Titlyanov EA. 1991. Comparisons of N- and P-limited productivity between high granitic islands versus low carbonate atolls in the Seychelles Archipelago: a test of the relative dominance paradigm. Coral Reefs. 10(4):199-209.

Lobitz B, Guild L, Montes M, Armstrong R,Goodman J. 2009. Pre-Processing of 2005 AVIRIS Data for Coral Reef Analysis. Paper, Proceedings of the 11th International Coral Reef Symposium, July 7-11, 2008, Fort Lauderdale, Florida.

Lubin D, Li W, Dustan P, Mazel CH, Stamnes K. 2001. Spectral signatures of coral reefs: features from space. Remote Sensing of the Environment 75:127-137.

Marshall PA and Baird AH. 2000. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19(2):155-163.

McClatchie S, Thorne RE, Grimes P, Hanchet S. 2000. Ground truth and target identification for fisheries acoustics. Fisheries Research. 47:173-191

Mendes JM and Woodley JD. 2002. Timing of reproduction in *Montastraea annularis*: relationship to environmental variables. Marine Ecology Progress Series. 227:241-251.

Miller J, Waara R, Muller E, Rogers CS. 2006. Coral bleaching and disease combine to cause extensive mortality on reefs in the U.S. Virgin Islands. Coral Reefs. 25(3):418

Mimura N and Nunn PD. 1998. Trends of beach erosion and shoreline protection in rural Fiji. Journal of Coastal Research. 14(1):37-46.

Mobley CD, Sundman LK, Davis CO, Bowles JH, Downes TV, Leathers RA, Montes MJ, Bissett WP, Kohler DDR, Raid RP, Louchard EM, Gleason A. 2005. Interpretation of hyperspectral remote-sensing imagery by spectrum matching and look-up tables. Applied Optics 44(17):3576-3592.

Moberg F and Folke C. 1999. Ecological goods and services of coral reef ecosystems. Ecological Economics. 29(2):215-233.

Muller EM, Rogers CS, Spitzack AS, van Woesik R. 2008. Bleaching increases likelihood of disease on Acropora palmata in Hawksnest Bay, St. John, US Virgin Islands. Coral Reefs 27(1):191-195.

Mumby PJ. 2006. The impact of exploiting grazers (*Scaridae*) on the dynamics of caribbean coral reefs. Ecological Applications. 16(2):747-769.

[NOAA] National Oceanographic and Atmospheric Administration. 2001. Endangered and Threatened Species: Endangered status for White abalone. [Internet]. [cited 2010 May 06]. Available from: http://www.nmfs.noaa.gov/pr/pdfs/fr/fr66-29046.pdf

[NOAA] National Oceanographic and Atmospheric Administration. 2006. Endangered and Threatened Species: Final Listing Determinations for Elkhorn and Staghorn Coral. [Internet]. [cited 2009 December 15]. Available from: http://www.nmfs.noaa.gov/pr/pdfs/fr/fr71-26852.pdf

[NOAA] National Oceanographic and Atmospheric Administration. 2008. Endangered and Threatened Species; Critical Habitat for Threatened Elkhorn and Staghorn Corals; Final Rule. [Internet]. [cited 2009 December 15]. Available from: http://www.nmfs.noaa.gov/pr/pdfs/fr/fr73-72210.pdf

[NOAA] National Oceanographic and Atmospheric Administration. 2009. Coral Reef Watch Program. [Internet]. [cited 2009 December 15]. Available from: http://coralreefwatch.noaa.gov/satellite/index.html.

[NOAA] National Oceanographic and Atmospheric Administration. 2010. Endangered and Threatened Wildlife; Notice of 90-Day Finding on a Petition to list 83 Species of Corals as Threatened or Endangered Under the Endangered Species Act. [Internet]. [cited

2010 February 25]. Available from: http://sero.nmfs.noaa.gov/pr/esa/pdf/75FR6616_90day_Finding_83_Corals.pdf

[NRC] National Research Council. 2001. Marine Protected Areas: Tools for sustaining ocean ecosystems. Washington, D.C.: National Academy Press.

Oxenford HA, Roach R, Brathwaite A, Nurse L, Goodridge R, Hinds F, Baldwin K, Finney C. 2008. Quantitative observations of a major coral bleaching event in Barbados, Southeastern Caribbean. Climatic Change. 87(3-4):435-449.

Paddock MJ, Cowen RK, Sponaugle S. 2006. Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. Coral Reefs 25(3):461-472.

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredas G, Warner RR, Jackson JBC. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science. 301(5635):955-958.

Peterson DL, Brass JA, Smith WH, Langford G, Wegener S, Dunagan S, Hammer P, Snook. 2003. Platform options of free-flying satellites, UAVs or the International Space Station for remote sensing assessment of the littoral zone. Int J Rem Sens 24:2785-2804.

Purkis SJ. 2005. A "reef-up" approach to classifying coral habitats from IKONOS imagery. IEEE Transactions on Geoscience and Remote Sensing 43(6):1375-1390.

Purkis SJ and Pasterkamp R. 2004. Interpreting in situ reef-top reflectance spectra with Landsat TM imagery to aid shallow-tropical benthic habitat mapping. Coral Reefs 23(1):5-20.

Rajasuriya A, Ranjith MW, Öhman MC. Coral reefs of Sri Lanka: human disturbance and management issues. 24(7/8):428-437.

Raymundo LJ, Couch CS, Bruckner AW, Harvell CD, Work TM, Weil E, Woodley CM, Jordan-Dahlgreen E, Willis BL, Sato Y, Aeby GS. 2008. Coral disease handbook: Guidelines for assessment, monitoring, and management. Raymundo LJ, Couch CS, Harvell CD (Eds.). Melbourne: Currie Communications.

Riegl B. 2003. Climate change and coral reefs: different effects in two high-latitude areas (Arabian Gulf, South Africa). Coral Reefs. 22(4):433-446.

Richards JA and Jia X. 2006. Remote Sensing Digital Image Analysis. Berlin: Springer-Verlag.

Richardson LL. 1998. Coral diseases: what is really known? Trends in Ecology & Evolution. 13(11):438-443.

Roberts CM. 1997. Connectivity and management of Caribbean coral reefs. Science 278(5342): 1454-1457.

Rogers CS. 1993. Hurricanes and coral reefs: the intermediate disturbance hypothesis revisited. Coral Reefs. 12(3-4):127-137.

Rohmann SO, Hayes JJ, Newhall RC, Monaco ME, Grigg RW. 2005. The area of potential shallow-water tropical and subtropical coral ecosystems in the United States. Coral Reefs. 24(3):370-383.

Rowlands GP, Purkis SJ, Riegl BM. 2008. The 2005 coral-bleaching event Roatan (Honduras): Use of Psuedo-invariants features in satellite assessments. 53(1):99-112.

Santer BD, Wigley TML, Gleckler PJ, Bonfils C, Wehner MF, AchutaRao K, Barnett TP, Boyle JS, Bruggemann, Fiorino M, Gillett N, Hansen JE, Jones PD, Klein SA, Meehl GA, Raper SCB, Reynolds RW, Taylor KE, Washington WM. 2006. Forced and unforced ocean temperatures in Atlantic and Pacific tropical cyclogenesis regions. Proceedings of the National Academy of Science of the United States of America. 103(38):13905-13910.

Schlager W. 2005. Carbonate sedimentology and sequence stratigraphy. Tulsa, Oklahoma: SEPM Foundation, Inc.

Sebens KP. 1994. Biodiversity of coral reefs: what are we losing and why? American Zoologist. 34(1):115-133.

Selig ER and Bruno JF. 2010. A global analysis of the effectiveness of marine protected areas in preventing coral loss. Public Library of Science ONE. 5(2):e9278.

Semesi AK, Mgaya YD, Muruke MHS, Francis J, Mtolera M, Msumi G. 1998. Coastal resources utilization and conservation issues in Bagamoyo, Tanzania. Ambio. 27(8):635-644.

Simpson MC, Scott D, New M, Sim R, Smith D, Harrison M, Eakin CM, Warrick R, Strong AE, Kouwenhoven P, Harrison S, Wilson M, Nelson GC, Donner S, Kay R, Geldhill DK, Lui G, Morgan JA, Kleypas JA, Mumby PJ, Palazzo A, Christensen TRL, Baskett ML, Skirving WJ, Brick C, Taylor M, Magalhaes, Bell J, Burnett JB, Turry MK, Overmas M, Robertson R. 2009. An overview of modeling climate change impacts in the Caribbean region with contribution from Pacific islands. United Nations Development Programme (UNDP). Barbados, West Indes.

Smith NP. 2001. Weather and hydrographic conditions associated with coral bleaching: Lee Stocking Island, Bahamas. Coral Reefs 20(4):415-422.

Sommerfield PJ, Jaap WC, Clarke KR, Callahan M, Hackett K, Porter J, Lybolt M, Tsokos C, Yanev G. 2008. Changes in coral reef communities among the Florida Keys, 1996-2003. Coral Reefs. 27(4):951-965.

Starr RM. O'Connel V, Ralston S. 2004. Movements of Lingcod (Ophiadon elongatus) in southeast Alaska: potential for increased conservation and yield from marine reserves. Can J Fish Aquat Sci 61:1083-1094

Steiner SCC and Kerr JM. 2008. Stony corals in Dominica during the 2005 bleaching episode and one year later. In Revista de Biologia Tropical, 56 (Supl. 1): International Journal of Tropical Biology. U.S. Virgin Islands: Association of Marine Laboratories of the Caribbean.

Stimson J, Sakai K, Sembali H. 2002. Interspecific comparison of the symbiotic relationship in corals with high and low rates of bleaching-induced mortality. Coral Reefs 21(4):409-421.

Suzuki A, Gagan MK, Fabricius KE, Yukino I, Kawahata H. 2003. Skeletal isotope microprofiles of growth perturbations in Porites colonies during the 1997-1998 mass bleaching event. Coral Reefs 22(4):357-369.

Szmant AM. 2002. Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline. Estuaries and Coasts. 25(4):743-766.

Szmant AM and Gassman NJ. 1990. The effects of prolonged "bleaching" on the tissue biomass and reproduction of the reef coral Montastraea annularis. Coral Reefs 8(4):217-224.

Veron JEN. 1995. Corals in space and time: the biogeography and evolution of the Scleractinia. Townsville, Australia: Australian Institute of Marine Science and CCR Qly Pty Ltd.

Veron JEN. 2000a. Corals of the World. Vol. 1. 3 vols. Townsville, Australia: Australian Institute of Marine Science and CCR Qly Pty Ltd.

Veron JEN. 2000b. Corals of the World. Vol. 2. 3 vols. Townsville, Australia: Australian Institute of Marine Science and CCR Qly Pty Ltd.

Veron JEN. 2000c. Corals of the World. Vol. 3. 3 vols. Townsville, Australia: Australian Institute of Marine Science and CCR Qly Pty Ltd.

Veron JEN, Hoegh-Guldberg O, Lenton TM, Loguh JM, Obura DO, Pearce-Kelly P, Sheppard CRC, Spalding M, Stafford-Smith MG, Rogers AD. 2008. The coral reef crisis: the critical importance of <350 ppm CO_2. Marine Pollution Bulliten. 58:1428-1436.

Vicente VP. 1990. Response of sponges with autotrophic endosymbionts during the coral bleaching episode in Puerto Rico. Coral Reefs 8(4):199-202.

Voss JD and Richardson LL. 2006. Nutrient enrichment enhances black band disease progression in corals. Coral Reefs 25(4):569-576.

Warren-Rhodes K, Sadovy Y, Cesar H. 2003. Marine ecosystem appropriation in the Indo-Pacific: a case study of the live reef fish food trade. Ambio. 32(7):481-488.

Whelan KRT, Miller J, Sanchez O, M Patterson. 2007. Impact of the 2005 coral bleaching event on Porites porites and Colpophyllia natans at Tektite Reef, US Virgin Islands. Coral Reefs 26(3):689-693.

Wiebe WJ, Johannes WJ, Webb KL. 1975. Nitrogen fixation in a coral reef community. Science. 188(4185):257-259.

Wilkinson C. 2008. Status of coral reefs of the world: 2008. Townsville, Queensland. Global Coral Reef Monitoring Network.

Wilkinson C, Chou LM, Gomez E, Ridzwan AR, Soekarno S, Sudara S. 1996. Status of coral reefs in Southeast Asia: threats and responses. 1996. 76(2):217.

Wilkinson C and Souter D. 2008. Status of Caribbean corals reefs after bleaching and hurricanes in 2005. Townsville, Australia: Global Coral Reef Monitoring Network, and Reef and Rainforest Centre.

Winter A, Appeldorn RS, Bruckner A, Williams, Jr. EH, Goenaga C. 1998. Sea-surface temperatures and coral bleaching off La Parguera, Puerto Rico. Coral Reefs 17(4):377-382.

Wood R. 1999. Reef Evolution. New York: Oxford University Press, Inc.

Woodley JD, Chornesky EA, Clifford PA, Jackson JBC, Kaufman LS, Knowlton N, Lang JC, Pearson MP, Porter JW, Rooney MC, Rylaarsdam KW, Tunnicliffe VJ, Whale CM, Wulff JL, Curtis ASG, Dallmeyer MD, Jupp BP, Koehl MAR, Neigel J, Sides M. 1981. Hurricane Allen's impact on Jamaican coral reefs. Science. 214(4522):749-755.

LANDSCAPE IMAGES FROM SITE 235 IN 2009

The following figures illustrate the benthic communities observed at one sampling site in the final year of the study. These images should provide the reader unfamiliar with the coral reef benthos a better understanding of the environment being sampled. Several important benthic cover classes are highlighted in each image including important scleractinian species, gorgonians, poriferans, macroalgae, and turf algae. From these images, the reader should understand that sampling benthic communities and detecting change within them is complicated by the spatial heterogeneity of the benthic organisms, the rugosity of the benthos, and the fluid environment in which divers must work.

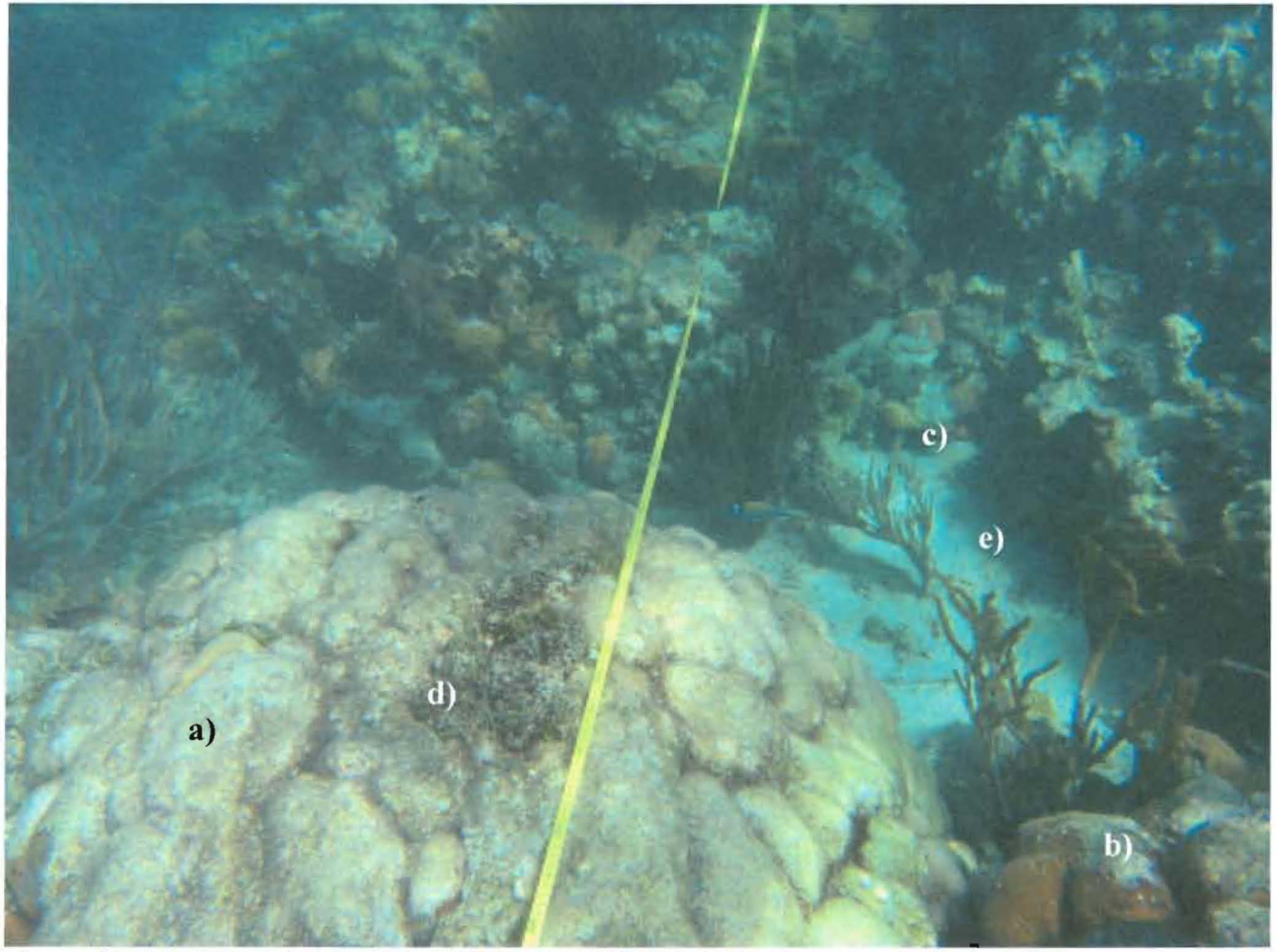

Figure 20: Landscape image from Site 235 in 2009 showing a) a mostly dead M. annularis colony covered by turf algae, b) poriferans, c) P. astreoides colonies, d) Halimeda thalli, and e) a sand patch. (Photo credit: Liane Guild 2009)

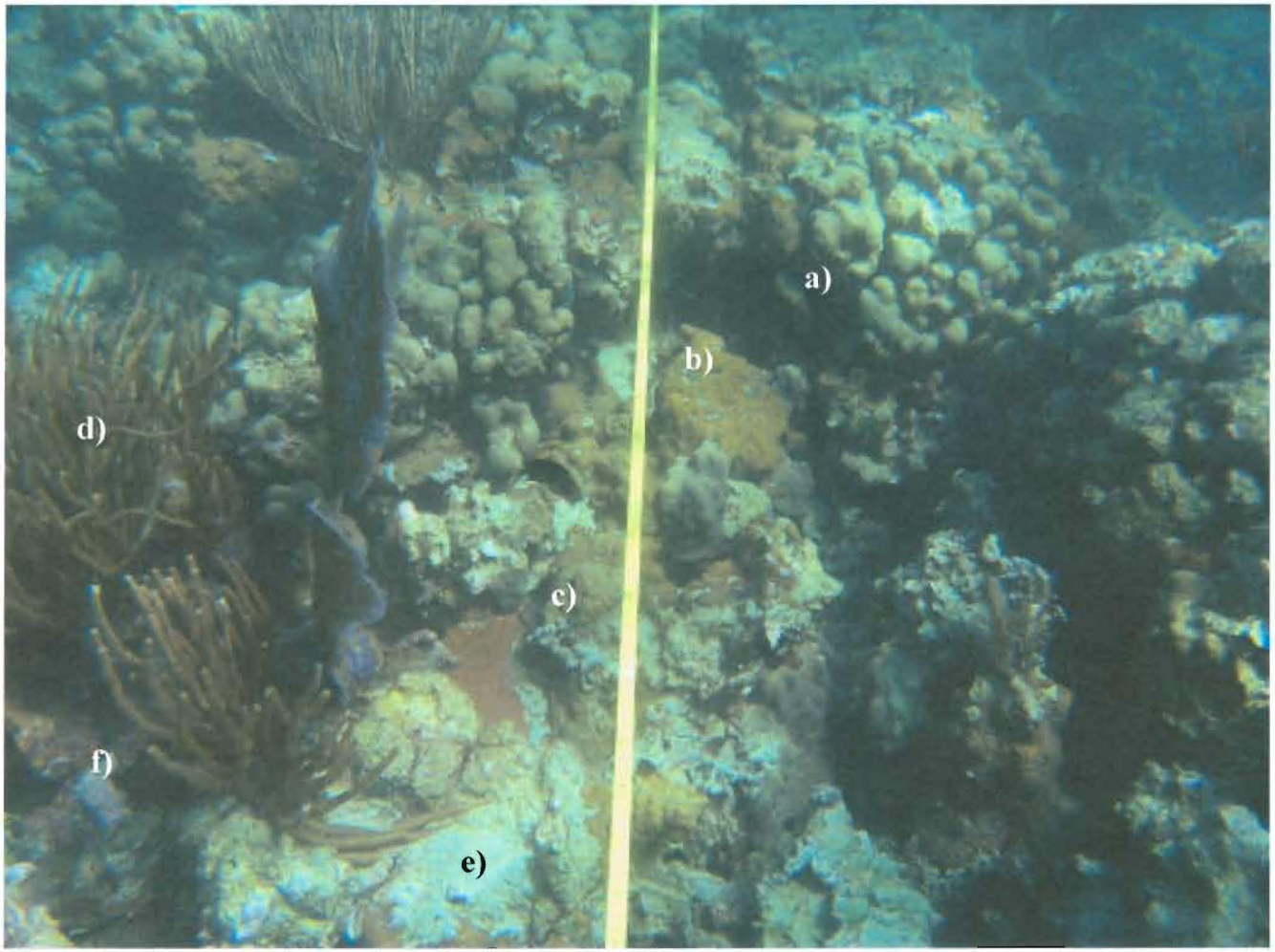

Figure 21: Landscape image from Site 235 in 2009 showing a) *M. annularis* colonies, b) poriferans, c) *P. astreoides* colonies, d) gorgonians, e) turf algae, and f) *Porolithon*. (Photo credit: Liane Guild 2009)

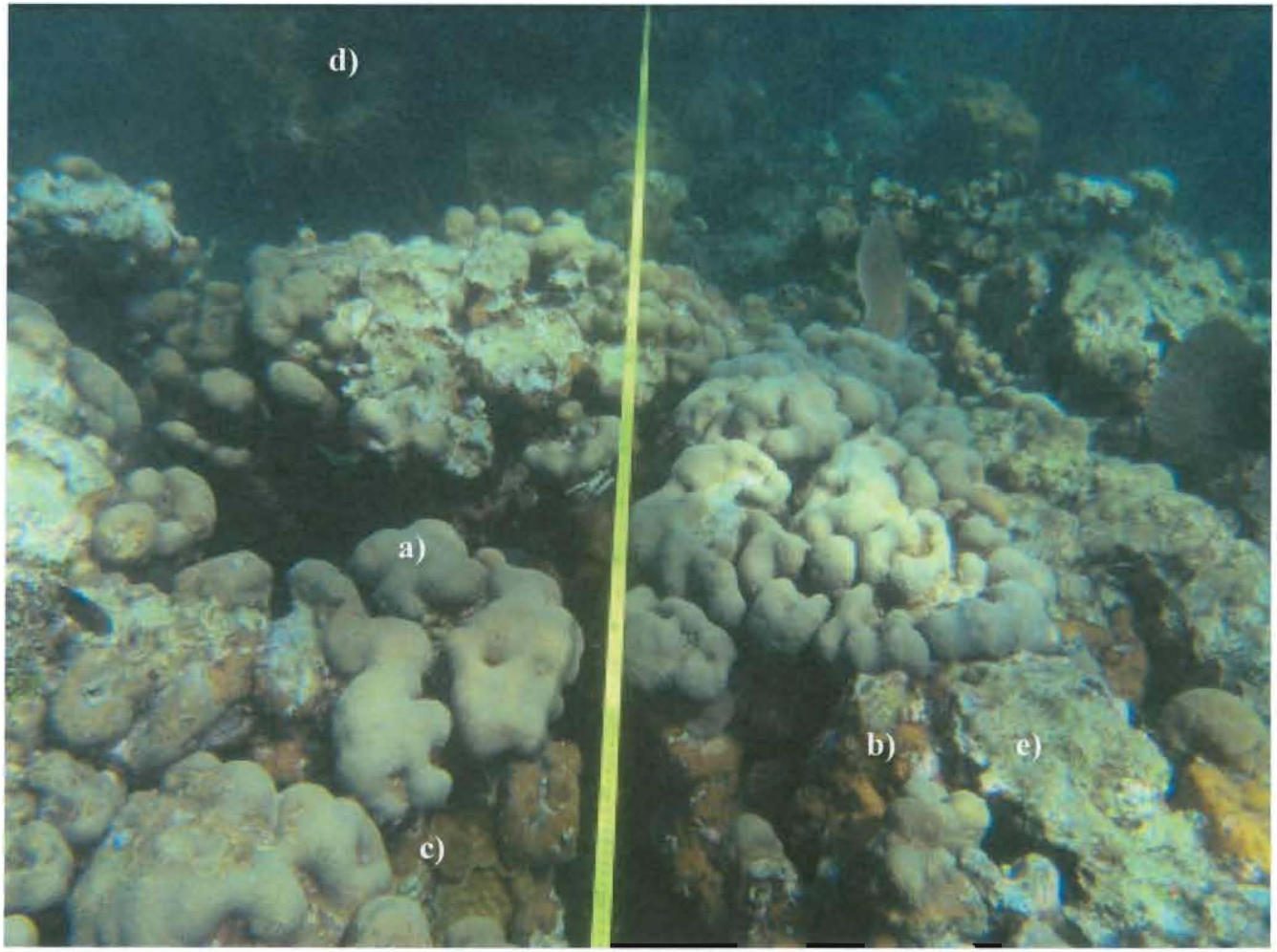

Figure 22: Landscape image from Site 235 in 2009 showing a) *M. annularis* colonies, b) poriferans, c) *P. astreoides* colonies, d) gorgonians, and e) turf algae. (Photo credit: Liane Guild 2009)

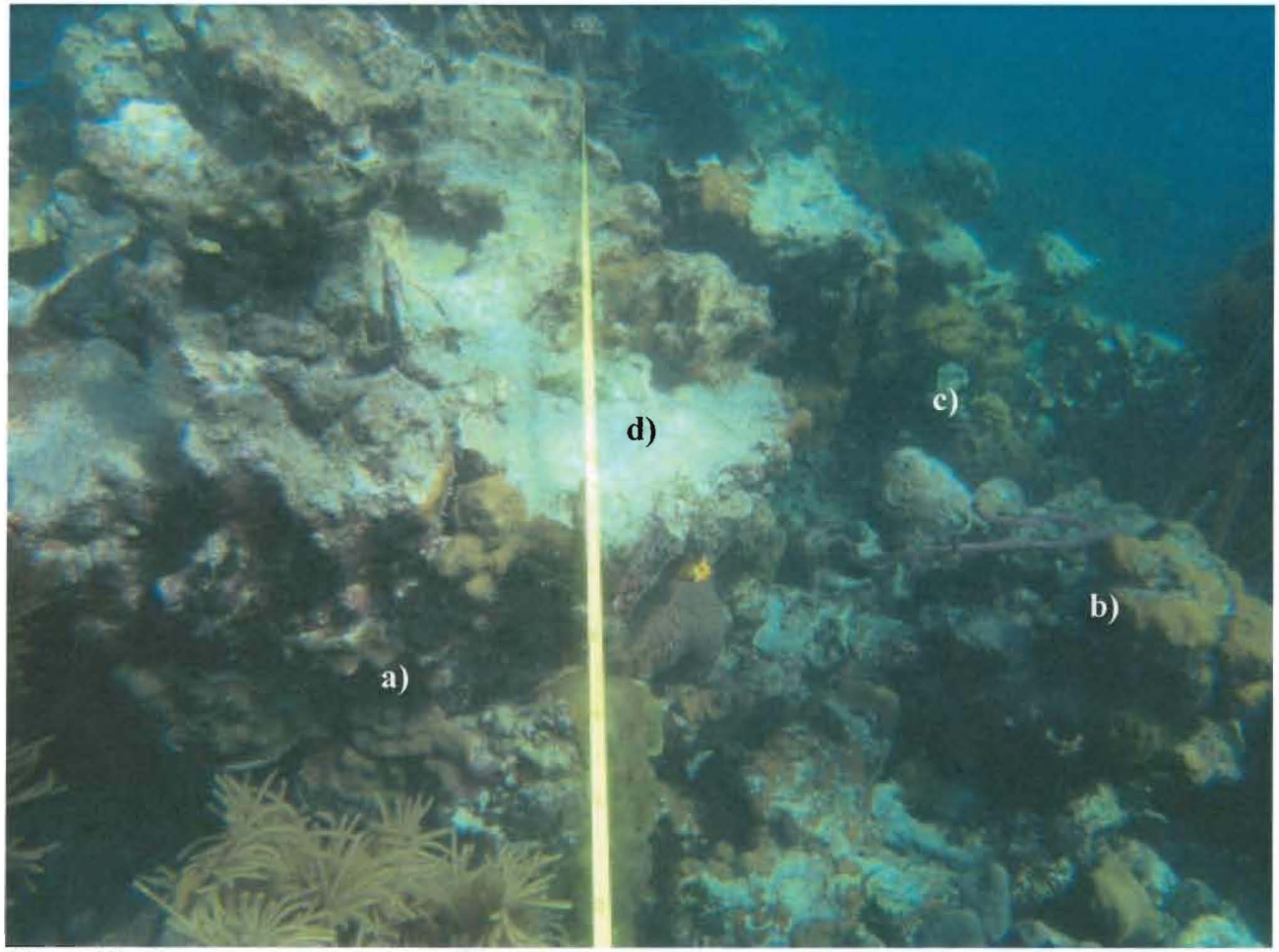

Figure 23: Landscape image from Site 235 in 2009 showing a) *M. faveolata* colonies (which are combined with *M. annularis* colonies for the analyses due to difficulty in distinguishing the two species in photoquadrats), b) poriferans, c) *P. astreoides*, and d) turf algae. (Photo credit: Liane Guild 2009)

R CODE FOR STATISTICAL ANALYSIS

The following R code forms the basis of the model-fitting process, which includes the creation of the spatial autocorrelation variable and the two models included in the model comparison to detect change. These commands were incorporated into the initial change detection for benthic cover classes and the sensitivity analyses. Commands used to read, format, write, or other otherwise alter the structure of data tables and matrices are excluded. Additionally, the only loop included is that used to create the spatial autocorrelation variable. Only the fundamental commands are included to enable to the reader to identify code useful for their own goals. That being said, those interested in viewing the full code can contact the author. Also, note that the symbol # indicates a comment.

```
# These two libraries must be loaded because the following commands rely on them.
library(spdep); library(spatial)

# This functions sets up the AIC table to be printed at the end of the process.
AICtable <- function( aic, n) {
 K <- aic$df
 AICc <- aic$AIC + 2 * K * (K+1) / ( n - K - 1 )
 delAIC <- AICc - min( AICc )
 AICw <- exp(-0.5*delAIC) / sum( exp(-0.5*delAIC))
 er <- max(AICw) / AICw
 data.frame( aic, AICc, delAIC , AICw, er)
}

# This function fits an exponential decay function to the correlogram.
f = function(p, correl){
  d = p[1]
  alpha = p[2]
  se = 1
  sse = sum( ( correl$y - expcov(correl$x, d=d, alpha=alpha, se=1 ))^2
)
return(sse)
}

# The following commands convert x (latitude), y (longitude), and year into the
# appropriate forms for model fitting. There are two sets of input variables; one for each
# year of data.
year1 <- ifelse(pt.data.2a$col.5a == yr_set1, 0, 1)
x1    <- pt.data.2a$col.10a - min(pt.data.2a$col.10a)
y1    <- pt.data.2a$col.11a - min(pt.data.2a$col.11a)

# Create the binary response variable (presence/absence) for the selected cover class.
response1 = ifelse(pt.data.2a$col.2a == cov_cls, 1, 0)


# Create the spatial autocovariance variable (sac.var). Note that the following commands
# are specific to a single year of data.

surface1 <- surf.ls(2,data.frame(x=x1, y=y1, z=response1))
```

```
cc1       = correlogram(surface1, 2000, plotit=F)
n         = length(response1)
mat1      = as.matrix(data.frame(x1,y1))
resp1     = response1
sac.var1 <- c(rep(0, n))
m1        = nlm( f=f, p=c(10,0.4), correl=cc1 )

for( u in 1:n){
  if( u < 5 | u %% 100==0) { print(u); flush.console() }
  sumw = 0
  sumwy = 0
  ivec = mat1[u,1:2]

  for( v in 1:n ){
      if( v == u ) next
      thresh = 100
      dx = ivec[1] - mat1[v,1]
      if( dx > thresh ) next
      dy = ivec[2] - mat1[v,2]
      if( dy > thresh ) next
      dist = sqrt( dx^2 + dy^2 )
      if( dist > thresh ) next
      w = expcov(dist, d=m1$estimate[1], alpha=m1$estimate[2], se=1)
      sumw = sumw + w
      sumwy = sumwy + w * resp1[v]
   }
  avey = sumwy / sumw
  sac.var1[u] = avey
}
```

Create the models that will be used to detect change.

```
M0 <- glm( response ~ sac.var, family = binomial(link="logit"),
data=pt.data.23)
M1 <- glm( response ~ sac.var + year, family = binomial(link="logit"),
data=pt.data.23)
```

Create the model selection table.

```
n_aic <- length(M0$residuals)
AICt  <- AICtable( AIC(M0, M1), n_aic )
```